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Studies on Estimation of Mortalities
I. Comparison of a Method Described by Beverton and Holt and a New Linear Formula[1]

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ABSTRACT

A method, described by Beverton (1954) and Beverton and Holt (1956 and 1957), giving estimates of the natural mortality rate, M, and the catchability coefficient, q, from catch at age and effort data, is examined. This method requires 4 to 5 iterations to arrive at the estimates. We have derived approximate solutions for q and M in a closed form. This makes the laborious iterations unnecessary, and gives virtually the same values as arrived at by iterations.

The effectiveness of the iterative Beverton and Holt method is evaluated by calculating q and M in 30 hypothetical examples. A new and simple (linear formula) method for estimating q and M is derived. Application of the new method to these 30 examples resulted in a 48% reduction in the standard deviation of q and a 45% reduction in that of M. The new method is in part the same as one suggested by Gulland, Beverton, and Holt (Beverton *et al.*, MS, 1958; Holt, MS, 1959) to arrive at initial values in their short-cut (iterative) method of estimating the mortality rates. Thus we show that these initial values are actually better estimates than the final values arrived at by the iteration.

Neither the Beverton and Holt method nor the linear formula give necessarily unbiased estimates; the bias depends on the types of variability in the data.

To arrive at non-biased, least squares estimates would require ancillary information not usually available on the distributions of the three variates: catch at age, effort, and catchability coefficient.

INTRODUCTION

Catch of fish at age depends on the abundance of fish at that age and on effort expended for fishing operations. Other factors influencing the catch include the behaviour of fish, their distribution, and particular techniques or strategies used by the fishing vessels. In estimating mortality rates, these latter factors are not generally assumed to affect the average relationship between the abundance of stock, the effort expended, and the resultant catch. There are exceptions. Thus Holt (MS, 1957) has considered the effect of co-operation among the fishing vessels on their fishing efficiency but in general such studies have not been carried far enough to assess their practical importance. To arrive at the well known average relationship, termed here the "catch equation" (cf. equation (4)), it has been stated that the fish or the fishing operations should be randomly distributed; moreover, their distributions should be independent (cf. Ricker, 1940, 1944; Beverton and Holt, 1956). Additional, while perhaps not so critical, assumptions are that fishing and natural mortality are spread evenly in time. The catch

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equation, based on the above assumptions, contains three unknown parameters: population size, what is called catchability coefficient, and instantaneous natural mortality rate; and two observed or directly estimated statistics: catch and effort.

The catch equation is basic to many estimation procedures in fisheries. DeLury (1947) used it to estimate the population size and the catchability coefficient. Silliman (1943) employed it to arrive at values of natural mortality rate. Silliman's method requires that the fishery be observed at two definitely different levels of fishing, each of at least two years' duration. More general methods for estimating the natural and fishing mortalities have been given by Widrig (1954), Beverton and Holt (1954, 1956), Fry (1949; MS, 1957), and Paloheimo (1958). The method employed by Widrig is similar to that by Beverton and Holt excepting that he does not carry the iterations beyond the first step. This iterative method is here referred to as the Beverton and Holt method, as they were first to describe it fully. The second method is referred to as the virtual population method, the name given to it by Dr Fry. Bishop (1959) has published a critique of the virtual population method. Her criticisms, however, were taken care of by the modification in the method by Paloheimo (1958).

The Beverton and Holt, and virtual population methods have been applied to few fisheries. The author is aware of only three fish stocks where the mortality rates have been so calculated. These are the Opeongo lake trout fishery (Beverton, 1954; Paloheimo, 1958), the Georges Bank haddock fishery (Taylor, 1958), and the South Bay bass fishery (Watt, 1959; this paper applies the earlier version of the virtual population method). Rounsefell's salmon data (Rounsefell and Kelez, 1938; Rounsefell, 1949) give rise to some difficulties, even if the Beverton and Holt method has been applied to it, due to the fact that Rounsefell's figures on escapement do not take account of the natural mortality rate.[2]

While applications of these general methods have not been very numerous, nevertheless, catch-per-effort data are widely collected, and apparently we may expect many more attempts to apply them.

Fisheries data are often subject to considerable sampling error and to deviations from the basic assumptions of the model. It is not always realized that before a method for estimating, say mortality rates, is developed, we must know the type of error inherent in the observation data. A method, which does not take account of such variability in data, may lead to biased estimates. Examination of the Beverton and Holt and virtual population methods shows that both are rather sensitive to the types of errors met in catch and effort data, and hence, may fail to give good estimates of the catchability coefficient and natural mortality rate; the bias is dependent on the type and magnitude of errors.

In the literature we find only descriptive accounts of the errors to which catch at age and effort data and the catchability coefficient are subject, and

[2]Beverton (personal communication) has pointed out that several other important applications of the Beverton and Holt method have actually been made. These include applications to East Anglian herring fishery (Cushing, 1959), and the Arctic cod and haddock fishery (Beverton *et al.*, MS 1959).

indeed, the estimation of error variances from field data does not seem feasible. Hence, any statistical method for estimating mortality rates may lead to somewhat biased estimates. The best method is the one which is least sensitive to types of variations met in fisheries data.

In this paper, we have concentrated on the study of the Beverton and Holt method. Its effectiveness has been calculated by estimating the catchability coefficient and natural mortality rate in 30 examples where random errors were introduced in the hypothetical data. In the examples considered, the method resulted in rather poor estimates of the natural mortality rate and of the catchability coefficient. The errors were large enough to warrant further examination. Since it was difficult to evaluate the effect of random errors in data on the estimates arrived at in successive iterations, we have derived approximate solutions of the natural mortality rate and catchability coefficient in a closed form. These solutions give approximately the same results as the iterative Beverton and Holt method, and they may be used to calculate the bias and standard deviations of the mortality estimates.

The method used to arrive at the approximate formulae may also be employed to derive an improved method for estimating the mortality rates. In the absence of a better name, the new method is termed here as the linear formula method. It is simple, requires no iterative procedure, and, in the examples calculated, resulted in a 48% reduction of the standard deviation of the catchability coefficient and a 45% reduction of the standard deviation of the natural mortality rate on the average.

The linear formula method has been suggested previously by Gulland, Beverton and Holt in some unpublished reports[3] (cf., Beverton *et al.*, MS, 1958; Holt, MS, 1959) as a means for arriving at initial values of the natural mortality rate and the catchability coefficients thereby reducing the number of iterations required. Thus our results show that these initial values are really better estimates than the iterative Beverton and Holt estimates.

Basic Concepts

The following concepts and notations will be used[4]:

- j subscript, refers to the j^{th} age group. We will simply take $j = 1$ or 2 as an index of relative age.
- n number of years.
- i subscript, refers to year i, $i = 1, \ldots\ldots, n$.
- $N_{j,i}$ numbers of the j-year-old fish at the start of the year i.
- $C_{j,i}$ numbers of j-year-old fish caught during the year i.
- f_i total effective effort during the year i.
- q catchability coefficient defined as the fraction of the population caught by one unit of effort; also the probability of capturing a fish. Subscript i or j will also be used for q to express its dependence on the year or the age.

[3]The author is obliged to both Holt and Beverton, who drew his attention to these reports when a draft of this current paper was submitted to them for comments.

[4]We are using the international notation (cf. Holt *et al.*, 1959).

M instantaneous natural mortality rate.

F_i instantaneous fishing mortality rate during the year i.

Z_i instantaneous total mortality rate during the year i.

t continuous time parameter, used primarily as a subscript.

N_t total remaining population size at time t, the original population being N_0.

f_t total effort from time $t = 0$ to time t.

C_t, Z_t, F_t are defined similarly.

$\hat{q}$, $\hat{M}$ estimates of q, M.

The above concepts warrant some comments. To define the effective fishing effort, we consider two different types of fisheries separately. First, those in which only one method of fishing and one type of boat is employed; fisheries of this kind will be referred to as simple fisheries. Second, those in which more than one method of fishing or more than one kind of boat is employed; these fisheries will be referred to as complex fisheries.

In the case of simple fisheries fishing a uniformly distributed fish stock, the effective effort is the actual effort measured in terms of hours fished, hauls made or lines fished. If the stock is not uniformly distributed, but, if the area may be divided into subareas where this is the case, the effective effort is the weighted average of the efforts expended in the subareas; the weighing factors are taken as proportional to the catches per unit of effort in the respective subareas. In complex fisheries, two or more different kinds of effort units are employed. Methods of calculating the effective effort, in such a case, have been studied by Gulland (1955), and Beverton and Holt (1957). We will not go into details here.

While the stock density may vary from subarea to subarea, we assume that the catchability coefficient is the same for all areas, subject perhaps only to random fluctuations.

The basic concepts introduced above are interrelated. The following formulae go back to Baranov (1918) and Ricker (1940, 1944):

$$N_t = N_0 e^{-Z_t} \tag{1}$$

$$F_t = qf_t \tag{2}$$

$$Z_t = qf_t + Mt \tag{3}$$

$$C_t = F_t N_0 (1 - e^{-Z_t})/Z_t \tag{4}$$

One of the basic assumptions implicit in the above equations is that fishing takes place independently of local concentrations of fish; i.e., that operators of the fishing vessels are not able to sense the presence of fish. In most commercial fisheries this is not the case. Thus, fish are detected by fish finders (loops), echo sounders, etc., and the prospects for a catch may be determined without actually making the haul. To what an extent this affects the basic equation is not known.

VARIATIONS IN THE BASIC PARAMETERS

To obtain unbiased estimates of parameters in a given (mathematical) relationship, a knowledge of the variability and observation errors inherent in the data is essential. In estimating mortality rates, our basic data are pairs of values C_{ji}, f_i. These data must be available at least for two age groups and for several years; the number of years required for a proper estimation depends on the accuracy of data. The parameters to be estimated are q and M. The relationship between these and the observational data (C_{ji}, f_i) from which q and M are estimated depends on the method. Thus the Beverton and Holt method uses different equations than the virtual population method.

The statistics C_{ji} and f_i are both subject to sampling error. Errors in C_{ji} may be due to errors in the total estimated weight of catch, in the estimated average weights, and in the estimated frequency of the j-year-olds. The total effort figure, f_i, is also subject to sampling error. In simple fisheries, it is a weighted average of efforts by subareas. The weighting factors should be proportional to the density of fish in each subarea; in practice, the catch per unit effort figures in each subarea are used. Hence, the total effort is only an estimate of what it is supposed to represent. In complex fisheries, the effort is a weighted total of efforts expressed in different units, the weighting factors being the sample estimates of the relative efficiencies of different units of effort.

Fluctuations in the catchability coefficient may be divided into systematic, long-term, short-term, and random variations. Systematic variations in q may result from a different behaviour pattern associated with the age or size of fish (Ricker, 1940; Gulland, 1955). Under long-term or short-term variations, we include the changes in q due to changes in weather, hydrographic conditions, etc. Properly random variations from the average value of q arise primarily from the random or contagious distribution of fish.

It is obvious that q is not constant but a variable. In estimating q we may only estimate its average value.

DESCRIPTION OF AND COMMENTS ON THE BEVERTON AND HOLT METHOD

Beverton and Holt derive from catch equation (4) their basic equations:

$$(5) \qquad qf_i + \mathrm{M} = \log_e\left(\frac{C_{1i}/f_i}{C_{2i+1}/f_{i+1}}\right) + \log_e\left(\frac{Z_i\,(1-e^{-Z_{i+1}})}{Z_{i+1}\,(1-e^{-Z_i})}\right)$$

If the catchability coefficient q is different at ages 1 and 2, then the above equation should read[5]:

$$(6) \qquad q_1 f_i + \mathrm{M} = \log_e\left(\frac{C_{1i}/q_1 f_i}{C_{2i+1}/q_2 f_{i+1}}\right) + \log_e\left(\frac{(q_1 f_i + \mathrm{M})\,(1-e^{-q_2 f_{i+1} - \mathrm{M}})}{(q_2 f_{i+1} + \mathrm{M})\,(1-e^{-q_1 f_i - \mathrm{M}})}\right)$$

Equation (5) contains the term $qf_i + \mathrm{M}$ on the left side; the right side is an estimate of Z_i; it depends on C_{1i}, C_{2i+1}, f_i, f_{i+1} as well as on q and M. We will denote this function by $Z'_i(C_{1i}, C_{2i+1}, f_i, f_{i+1}, q, \mathrm{M})$ or simply by Z'_i.

[5]The term $\log_e(q_2/q_1)$ was accidentally omitted in Paloheimo, 1958, page 752.

Rewriting (5) in the abbreviated notation, we get:

$$(5')\quad qf_i + M = Z'_i(C_{1i}, C_{2i+1}, f_i, f_{i+1}, q, M)$$

To estimate the values of q and M in equation (5') from the statistics on catch and effort, an iterative procedure is used. Initial values of q and M are first guessed at, or estimated, from the regression of $\log_e(C_{1i}/f_i)/(C_{2i+1}/f_{i+1})$ on f_i (cf. (5)) as the slope of the line (q) and the intercept (M) at zero effort. The initial values of q and M are then used to calculate new values of Z'_i and a new regression line of Z'_i on f_i is obtained. The slope of the line and the intercept at $f = 0$ are the new estimates of q and M respectively. Substituting the new values of q and M in the expressions for Z'_i gives improved estimates for Z'_i which may be used in turn to arrive at a new regression line and improved estimates of q and M. The iteration is continued until the resulting q and M converge to fixed values which are then the final estimates of q and M.

BIAS IN THE MORTALITY ESTIMATES. Successive estimates of q and M, at each iteration, are given by the slope and the intercept, at $f = 0$, of the regression line of Z'_i on f_i. Substituting f_i and Z'_i in the familiar regression formula, we get:

$$(7)\quad \hat{q} = \frac{(n-1)\ (\Sigma f_i Z'_i) - (\Sigma f_i)\ (\Sigma Z'_i)}{(n-1)\ (\Sigma f_i^2) - (\Sigma f_i)^2} \qquad \hat{M} = \frac{(\Sigma f_i^2)\ (\Sigma Z'_i) - (\Sigma f_i)\ (\Sigma Z'_i f_i)}{(n-1)\ (\Sigma f_i^2) - (\Sigma f_i)^2}$$

where summations are from $i = 1$ to $i = n-1$.

It is well known that the use of regression techniques in fitting the straight line $Z'_i = qf_i + M$ assumes that f is free of error and q is constant. Deviations from these assumptions will lead to bias in the estimate of the slope and intercept of the line. Further complications result because of the fact that Z'_i is dependent on f_i, f_{i+1}, q, and M.

For a discussion of different techniques of fitting a straight line, we refer to Kendall (1957), Williams (1959) and Madansky (1959). If both Z'_i and f_i are subject to error, $Z'_i = qf_i + M$ is not a regression model but a functional relationship and an entirely different technique should be used to arrive at the estimates of q and M. If nothing more about f_i and Z'_i is known than their observed or calculated values, the line cannot be properly fitted. Efficient techniques of fitting a straight line, when errors in Z'_i and in f_i are not independent but correlated, are not known.

Let Δf_i and Δq_i denote possible error in f_i or relative variation in q (i.e., $q_i = q(1 + \Delta q_i)$. Consider first, the case when f_i is subject to observational error. Then, in equation (7), the term $(n-1)\Sigma f_i^2$, originally assumed to be without error, has actually been inflated by $(n-1)\mathrm{var}\Delta f$ and the term $(n-1)\Sigma f_i Z'_i$ by $(n-1)\mathrm{cov}(Z, \Delta f)$. These correction terms should be subtracted from the corresponding terms $(n-1)\Sigma f_i^2$ and $(n-1)\Sigma f_i Z'_i$ to arrive at non-biased estimates of q and M for fixed values of Z'_i.

In the case where q is variable but f_i is free of error, considerations similar to those above apply. We may write $q_i f_i = q(1 + \Delta q_i)f_i$ and consider that the error actually occurs in f_i, f_i being the observed value and $(1 + \Delta q_i)f_i$ its true

value. Minor deviation results in the fact that the variance of f_i is now correlated with f_i. Hence, the term $(n-1)\Sigma f_i^2$ must be decreased by the factor $(1 + \text{var}\Delta q)$ and the term $(n-1)(\Sigma f_i Z'_i)$ by the additive constant $(n-1)\text{cov}(1 + \Delta q, Z')$ to arrive at non-biased estimates of (the average) q and M.

Formula (7) results in efficient and unbiased estimates of q and M for fixed Z'_i only when the regression model strictly applies. When it does not, additional components of error in q and M are introduced by having the values of q and M on the right side of (5) fixed (in Z'_i) while fitting the regression line of Z'_i on f_i and, also, by the fact that the errors in the right and left side of (5) are not independent. This may be seen from the approximate formulae we will derive for the Beverton and Holt iterative estimates.

APPROXIMATION FOR EQUATION (5). Equation (5), which Beverton and Holt solve by iterative methods, may be solved approximately in a closed form. We first write equation (5) in the form:

$$qf_i + M = I_i + K_i = Z'_i \tag{8}$$

where:

$$I_i = \log_e\left(\frac{C_{1i}/f_i}{C_{2i+1}/f_{i+1}}\right)$$

$$K_i = \log_e\left(\frac{Z_i(1-e^{-Z_i+1})}{Z_{i+1}(1-e^{-Z_i})}\right)$$

We may approximate K_i by a simple expression:

$$K_i \sim -\frac{Z_{i+1}}{2} + \frac{Z_i}{2} \tag{9}$$

where we have written:

$$-\log_e \frac{1-e^{-Z}}{Z} \sim \frac{Z}{2} \tag{10}$$

by expanding $\log_e(1-e^{-Z})/Z$ as an infinite series and retaining only the first term. In Table I we have tabulated the values of $-\log_e(1-e^{-Z})/Z$ and of $Z/2$ for $0.10 \leq Z \leq 1.00$. Between the values $0.2 \leq Z \leq 1.00$, which is the likely range

TABLE I. Values of $\log_e(1-e^{-Z})/Z$.

Z	Z/2	$-\log_e(1-e^{-Z})/Z$	Z	Z/2	$-\log_e(1-e^{-Z})/Z$
0.10	0.05	.0492	0.60	0.30	.2850
0.20	0.10	.0982	0.70	0.35	.3297
0.30	0.15	.1462	0.80	0.40	.3724
0.40	0.20	.1933	0.90	0.45	.4165
0.50	0.25	.2395	1.00	0.50	.4587

Note: $\dfrac{\sum_{Z=0.20}^{Z=1.00} \log_e(1-e^{-Z})/Z}{0.20+0.30+\ldots+0.90+1.00} \sim 0.47$

for most mortality estimates, the values of Z/2 are somewhat higher than those of $-\log_e(1-e^{-Z})/Z$. Thus if we write in general:

$$-\log_e \frac{1-e^{-Z}}{Z} \sim aZ \tag{10'}$$

$$K_i \sim -aZ_{i+1} + aZ_i \tag{9'}$$

the best value for "a" varies slightly depending on the range of the Z_i values. While for all practical purposes we could take $a = 0.5$ in applications, nevertheless, a somewhat smaller value of "a" gives a slightly better approximation. We have chosen $a = 0.47$, which is its average value between $0.2 \leq Z \leq 1.00$, obtained from Table I by calculating:

$$a = \frac{-\Sigma \log_e(1-e^{-Z_i})/Z_i}{\Sigma Z_i} \tag{11}$$

where the summation is over the values of $Z_i = 0.2, 0.3, \ldots 0.9, 1.0$.

Equations (8) and (9') allow us to approximate the basic Beverton and Holt equation in the form:

$$\begin{aligned} qf_i + M &= I_i + a(Z_i - Z_{i+1}) \\ &= I_i + qa(f_i - f_{i+1}) = Z'_i \end{aligned} \tag{12}$$

The iterative procedure to estimate q and M in (5) leads to estimates of q and M which, when substituted in (7), satisfy it. Hence, substituting approximations (12) in (7), the final value of q satisfies.

$$\hat{q} = \frac{(n-1)(\Sigma f_i I_i)-(\Sigma f_i)(\Sigma I_i)-\hat{q}a(\Sigma f_i)(f_1-f_n)+\hat{q}(n-1)a[\Sigma f_i(f_i-f_{i+1})]}{(n-1)\Sigma f_i^2-(\Sigma f_i)^2}$$

From this we may solve for $\hat{q}$:

$$\hat{q} = \frac{(n-1)(\Sigma f_i I_i)-(\Sigma f_i)(\Sigma I_i)}{(n-1)(\Sigma f_i^2)-(\Sigma f_i)^2+a(\Sigma f_i)(f_1-f_n)-(n-1)a[\Sigma f_i(f_i-f_{i+1})]} \tag{13}$$

Summations are from $i = 1$ to $i = n-1$

When the value of $\hat{q}$ obtained from (13) and approximation (12) for Z'_i are substituted in expression (7) for $\hat{M}$, we get:

$$\hat{M} = \frac{(\Sigma f_i^2)(\Sigma I_i)-(\Sigma f_i)(\Sigma f_i I_i)+qa(\Sigma f_i^2)(f_1-f_n)-qa(\Sigma f_i)[\Sigma f_i(f_i-f_{i+1})]}{(n-1)(\Sigma f_i^2)-(\Sigma f_i)^2} \tag{14}$$

Equations (13) and (14) provide satisfactory approximations to the iterative solution of equation (5) by Beverton and Holt in all cases where the iteration converges. Since (13) and (14) give solutions for q and M in a closed form, calculating time is reduced appreciably.

EXAMPLE I.

In Table II we have calculated, using data from Tables IX and X, the Beverton and Holt iterative estimates and the approximate estimates (13) and

(14) with $a = 0.47$. The maximum difference between the iterative estimates and the approximate estimates for M is 0.023 and for q is 0.004.

TABLE II. Comparison of Beverton and Holt iterative solutions of q and M and the approximate solutions of q and M by formulae (13) and (14). Data are given in Tables IX and X.

	Beverton and Holt		Approximate	
Example No.	$\hat{q}$	$\hat{M}$	$\hat{q}$	$\hat{M}$
1	.073	.354	.075	.344
2	.071	.334	.073	.326
3	.119	.091	.122	.076
4	.210	−.389	.206	−.363
5	.008	.774	.008	.752
6	.091	.225	.094	.213
7	.122	.059	.125	.046
8	.127	.052	.129	.038
9	.054	.455	.055	.447
10	.155	−.094	.158	−.115

THE NEW LINEAR FORMULA

Equation (12) suggests a rather simple method for calculating $\hat{q}$ and M. By taking $a = \frac{1}{2}$ we may write the equation in the following form:

$$q\,\tfrac{1}{2}(f_i+f_{i+1})+M = I_i$$
$$I_i = \log_e \frac{C_{1i}/f_i}{C_{2i+1}/f_{i+1}} \tag{15}$$

Regression estimates for q and M from (15) are now given by:

$$\hat{q} = \frac{(n-1)(\Sigma \bar{f}_i I_i)-(\Sigma \bar{f}_i)(\Sigma I_i)}{(n-1)(\Sigma \bar{f}_i{}^2)-(\Sigma \bar{f}_i)^2}$$
$$\hat{M} = \frac{(\Sigma \bar{f}_i{}^2)(\Sigma I_i)-(\Sigma \bar{f}_i)(\Sigma \bar{f}_i I_i)}{(n-1)(\Sigma \bar{f}_i{}^2)-(\Sigma \bar{f}_i)^2} \tag{16}$$

where $f_i = \frac{1}{2}(f_i + f_{i+1})$ and the summation is taken from $i = 1$ to $i = n-1$. If, in place of approximation (10) we use (10′), $\bar{f}_i = \frac{1}{2}(f_i + f_{i+1})$ should be replaced by $\bar{f}_i = (1-a)f_i + af_{i+1}$ where we could take $a = .47$. In practice, however, there seems to be so little difference between the results obtained by using the two alternatives for $\bar{f}_i$ that we have preferred the one which is algebraically simpler (i.e., $\bar{f}_i = \frac{1}{2}(f_i + f_{i+1})$).

COMPARISON OF THE BEVERTON AND HOLT METHOD AND THE NEW LINEAR FORMULA

Neither the Beverton and Holt (formulae (13) and (14)) or the linear formula method (16) give unbiased estimates of the mortality rates. Indeed, unbiased estimates cannot be obtained unless we know a good deal more of the under-

lying statistical nature of our data than is available from current fisheries data. In general, however, the estimates (16) are less biased and have a smaller variance than those obtained from (13) and (14).

The variance for $\hat{q}$ and $\hat{M}$ can be calculated from (13), (14) and (16). It should be noted that the often-used variance estimates (cf. Taylor, 1958; Beverton, 1954) obtained from the least squares fit of Z'_i on f_i are not valid estimates of the variance of $\hat{q}$ and $\hat{M}$.

To avoid cumbersome formulae we rewrite the approximate Beverton and Holt equations (13) and (14) as follows:

$$\hat{q} = \frac{D_1}{D_2};\ \hat{M} = \frac{E_1 + \hat{q}E_2}{E_3} \tag{17}$$

using substitutions D_1, E_1, E_2, and E_3 for their obvious equivalents in the original formulae. For the linear formula estimates of q and M, written now as $\hat{\bar{q}}$ and $\hat{\bar{M}}$ to distinguish them from $\hat{q}$ and $\hat{M}$ in (17), we put similarly:

$$\hat{\bar{q}} = \frac{\bar{D}_1}{\bar{D}_2};\ \bar{M} = \frac{\bar{E}_1}{\bar{E}_3} \tag{18}$$

Expansion for $\bar{D}_1$, $\bar{D}_2$, $\bar{E}_1$, and $\bar{E}_3$ can be obtained from (16).

The general order of magnitude of D_1, D_2, E_1 and E_3 is about the same as that of $\bar{D}_1$, $\bar{D}_2$, $\bar{E}_3$. A term equivalent to E_2 does not appear in the expression for $\bar{M}$; E_2 can be either positive or negative.

To compare the variance of $\hat{q}$ and $\hat{M}$ with those of $\hat{\bar{q}}$ and $\hat{\bar{M}}$, we distinguish four different possibilities, depending on whether (a) catches at age or (b) effort figures are subject to sampling error, or (c) the catchability coefficient is variable or finally (d) whether any combination of these three cases occurs.

If the catches at age data are the only observational data subject to sampling error and if the catchability is strictly constant, then formula (16) may not have any advantages over the Beverton and Holt method or formulae (13) and (14), because the variances of D_1, and E_1 are about the same as those of the corresponding expressions $\bar{D}_1$, and $\bar{E}_1$ and the covariance between $\hat{q}E_2$ and E_1 could possibly be negative and by absolute value as large as $\mathrm{var}(\hat{q}E_2)$ (cf. (17)).

In all other cases, linear formula (16) has a definite advantage over the Beverton and Holt method or, what is the same thing, over formulae (13) and (14). This follows simply from the fact that we have replaced f_i in formulae (13) and (14) by:

$$\bar{f}_i = \tfrac{1}{2}(f_i + f_{i+1})$$

That is, if f_i's are subject to sampling error while C_{ji}'s are observed without error and q is constant then, since:

$$\mathrm{var}\bar{f}_i = \tfrac{1}{4}(\mathrm{var}f_i + \mathrm{var}f_{i+1}) \sim \tfrac{1}{2}\mathrm{var}f_i$$

the variances of $\bar{D}_1$ and $\bar{E}_1$ are reduced to about half of those of D_1 and $E_1(+qE_3)$. The variances of $\bar{D}_2$ and $\bar{E}_2$, compared with the variances of D_2 and E_2, respectively, are reduced by more than half. This is because the $\bar{f}_i$'s and the

f_i's appear as squares or cross products in $\overline{D}_2$, D_2, $\overline{E}_2$ and E_2. Thus the variances of $\hat{\bar{q}}$ and $\hat{\bar{M}}$ are, in turn, reduced by more than half from those of $\hat{q}$ and $\hat{M}$.

If q is subject to variation, the linear formula still has similar advantages because we may put $q_i = q(1 + \Delta q_i)$ but consider that, instead of error being in q, it is the f_i's which are observed with error, the observed value being f_i and the true value $(1 + \Delta q_i)f_i$.

In the last case, when all three possible types of error are present, formula (16) has still advantage over (13) and (14) although the variances may not be reduced as much as before.

The improvement in the mortality estimates, which results from use of the linear formula (16), can be demonstrated by hypothetical examples.

EXAMPLE II. f_i's SUBJECT TO ERROR

In this example, we have let $q = 0.10$ and $M = 0.10$, and calculated hypothetical catches for two years from 100,000 recruits each year, for a 10-year period. The values of f_i were allowed to vary between 4 and 8 units but were otherwise randomly picked from a table of random numbers. The values of f_i and the resulting catches are tabulated in Table III.

TABLE III. Hypothetical catches for 2 successive years from 100,000 recruits each year, over a 10-year period, with $q=0.10$ and $M=0.10$ and with expended efforts as shown.

		Catch	
Year	Effort	1st year	2nd year
1	4.00	31,476	
2	4.00	31,476	19,090
3	8.00	52,752	31,994
4	8.00	52,752	21,449
5	6.00	43,146	17,543
6	4.00	31,476	15,631
7	5.00	37,600	22,804
8	4.00	31,476	17,274
9	8.00	52,752	31,994
10	7.00	48,181	19,590

To introduce "observation error" in f_i's in Table III, random normal deviates, read off from a table of random normal deviates (Deming, 1946) were added, properly scaled, to each f_i. The deviates, as read off from the table, were multiplied by $\frac{1}{2}$ to reduce the standard deviation of the error component to $\frac{1}{2}$ unit. Ten sets of (ten) f_i's, $i = 1, \ldots, 10$ were so picked, giving in conjunction with the C_{ji}'s 10 examples, each containing 10 years' hypothetical catch and effort data. The "estimated" efforts are tabulated in Table IV.

TABLE IV. Hypothetical fishing efforts. Figures obtained from the efforts in Table III by adding to each effort a random normal deviate with standard deviation 0.5.

	Example									
Year	1	2	3	4	5	6	7	8	9	10
1	4.09	5.14	3.65	3.33	3.89	4.22	3.30	4.14	5.11	4.01
2	3.89	3.47	3.72	3.27	3.43	4.64	3.49	3.48	3.89	3.82
3	7.94	7.66	7.82	8.04	8.36	8.28	7.36	7.65	7.44	7.47
4	7.95	7.23	9.08	7.93	8.09	8.37	7.41	7.63	8.38	8.10
5	6.22	5.81	7.06	6.70	5.18	6.19	6.05	6.62	6.00	5.21
6	4.20	3.08	4.42	4.46	3.31	4.44	4.09	3.57	4.30	4.48
7	4.52	4.91	3.56	5.04	4.81	5.63	5.33	4.85	5.05	5.23
8	3.44	3.41	3.79	4.61	3.86	4.23	3.52	3.07	4.31	3.85
9	8.01	7.88	7.60	9.04	8.55	7.78	8.29	8.14	7.87	8.44
10	7.39	6.59	7.02	6.58	6.73	6.01	7.37	6.71	6.76	8.04

The Beverton and Holt method and the linear formula (16) were applied to catches in Table III, and to the sets of efforts in Table IV, to arrive at the estimates of q and M. The correct values of q and M are $q = 0.10$ and $M = 0.10$. In applying the Beverton and Holt method[6], the iterations were continued until the successive estimates of M changed less than .01 or of q less than .001. This usually required 4 or 5 iterations. The results are tabulated in Table V. It is to be noted that the linear formula (16) results in estimates of q and M, the variances of which, calculated from the known values of $q = 0.10$ and $M = 0.10$, are about 40% smaller for $\hat{q}$ and 38% smaller for $\hat{M}$ than the corresponding variances using the Beverton and Holt method.

TABLE V. Comparison of Beverton and Holt estimates and linear formulae estimates of q and M. Data are from Tables III and IV. The true values are $q = 0.10$ and $M = 0.10$.

	Beverton and Holt estimate		Linear formulae estimate	
Example	$\hat{q}$	$\hat{M}$	$\hat{q}$	$\hat{M}$
1	.100	.111	.123	−.026
2	.031	.475	.130	−.098
3	.078	.242	.103	.092
4	.051	.389	.074	.252
5	.028	.523	.072	.270
6	.107	.011	.096	.136
7	.073	.295	.111	.083
8	.050	.394	.143	−.131
9	.138	−.166	.147	−.220
10	.093	.156	.110	.052
Standard deviation of the estimates from the true value	.042	.251	.025	.155

[6]A LGP-30 computer was used.

EXAMPLE III. f_i's SUBJECT TO ERROR

Data in Tables VI and VII are obtained the same way as the data tabulated in Tables III and IV respectively except that we have used $q = 0.10$ and $M = 0.20$ in arriving at the hypothetical catches at age.

TABLE VI. Hypothetical catches for 2 years from 100,000 recruits each year over a 10-year period, with $q=0.10$ and $M=0.20$, and with expended efforts as shown.

		Catch	
Year	Effort	1st year	2nd year
1	7.00	46,158	
2	6.00	41,298	16,792
3	5.00	35,955	15,155
4	4.00	30,080	14,938
5	5.00	35,955	19,732
6	4.00	30,080	14,938
7	6.00	41,298	22,664
8	5.00	35,955	16,155
9	7.00	46,158	22,922
10	8.00	50,568	20,561

TABLE VII. Hypothetical fishing efforts. Figures obtained from the efforts in Table VI by adding to each effort a random normal deviate with mean zero and standard deviation 0.5.

	Example No.									
Year	1	2	3	4	5	6	7	8	9	10
1	7.98	7.94	7.32	5.54	7.86	6.55	5.87	6.56	6.67	7.31
2	6.78	6.71	6.59	6.77	5.96	5.12	6.22	6.07	5.00	5.65
3	4.41	4.82	5.13	4.75	5.65	5.08	4.64	5.45	4.74	5.52
4	3.27	3.88	3.88	3.49	3.52	3.46	4.03	3.93	4.34	3.00
5	5.18	4.88	4.85	4.61	5.46	4.94	5.17	4.80	5.03	4.65
6	3.47	4.29	3.83	3.51	3.24	3.80	3.93	3.75	3.41	3.67
7	6.27	6.64	6.27	6.09	6.35	6.22	5.54	5.76	5.86	5.96
8	4.77	4.71	4.31	5.66	5.61	5.02	5.51	5.68	4.38	4.62
9	7.41	6.99	7.10	7.15	7.20	7.54	6.80	7.67	6.54	7.38
10	8.58	7.81	8.64	7.29	8.18	6.63	7.68	8.13	8.16	8.87

Application of the two methods considered here gives the values of $\hat{q}$ and $\hat{M}$ tabulated in Table VIII. The results confirm the conclusions from Example II, with 67% and 69% reductions in the standard deviations of $\hat{q}$ and $\hat{M}$, respectively, using the linear formula.

TABLE VIII. Comparison of Beverton and Holt estimates and linear formulae estimates of q and M. Data from Tables VI and VII. The true values are $q = 0.10$ and $M = 0.20$.

	Beverton and Holt estimates		Linear formulae estimates	
Example	$\hat{q}$	$\hat{M}$	$\hat{q}$	$\hat{M}$
1	−.007	.780	.069	.363
2	.029	.564	.067	.354
3	.046	.498	.108	.153
4	.021	.653	.079	.337
5	−.026	.886	.083	.269
6	−.024	.865	.038	.535
7	.110	.174	.105	.194
8	.084	.285	.081	.301
9	.035	.574	.119	.139
10	.007	.718	.089	.276
Standard deviation of the estimates from the true value	.084	.457	.028	.144

EXAMPLE IV. q SUBJECT TO VARIATION

In this set of examples, we have allowed q to vary from year to year in a random manner by adding random normal deviates of standard deviation 0.01 to the basic value $q = 0.10$. The resulting q's are tabulated in Table IX. The hypothetical effort figures and the catches, corresponding to these efforts and catchability coefficients in Table IX, are tabulated in Table X.

TABLE IX. Hypothetical values of the catchability coefficient, q. Each figure is obtained by adding to $q = 0.10$ a random normal deviate with mean zero and standard deviation 0.01.

	Example No.									
Year	1	2	3	4	5	6	7	8	9	10
1	.0946	.0931	0.959	.1060	.0975	.0932	.1040	.0999	.0988	.1100
2	.1167	.0854	.1061	.1093	.1004	.0992	.0858	.1097	.1077	.0806
3	.0959	.1072	.0855	.0962	.1060	.0877	.1115	.1210	.1002	.1007
4	.1028	.1073	.1037	.0883	.1084	.1002	.0930	.0870	.1137	.0989
5	.1053	.1009	.0991	.0969	.0864	.0978	.0908	.0944	.0871	.1042
6	.1030	.0914	.0963	.0944	.1065	.1091	.1005	.0805	.0776	.1135
7	.1001	.1022	.1081	.1038	.0870	.1166	.1138	.1063	.0951	.1111
8	.1056	.0931	.1008	.0943	.0950	.0920	.0854	.0998	.1191	.1023
9	.1046	.0904	.0973	.1073	.0908	.0940	.0939	.0955	.0924	.1234
10	.1084	.0966	.0956	.0888	.1004	.1053	.1154	.1012	.0931	.0958

TABLE X. Hypothetical efforts and catches. Catch figures are calculated for 2 years from 100,000 recruits each year over a 10-year period, using effort figures and catchability coefficients varying randomly with each year and example. Catchability coefficients are given in Table IX, and M = 0.20. C_1 is catch at age 1; C_2 is catch at age 2.

Example No.:	1		2		3		4		5	
Effort	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2
7.00	44,366	...	43,887	...	44,789	...	48,065	...	45,366	...
6.00	46,153	19,490	36,623	15,620	43,151	18,063	44,081	17,183	41,404	17,121
5.00	34,828	14,161	37,935	18,615	31,779	18,760	34,885	14,819	37,615	16,867
4.00	30,747	15,576	31,857	15,253	30,986	16,537	27,116	13,723	32,139	15,488
5.00	37,441	20,327	36,231	19,318	35,739	19,328	35,118	20,200	32,017	18,985
4.00	30,806	14,895	27,954	13,815	29,155	14,534	28,716	14,473	31,657	16,829
6.00	41,349	22,428	41,952	23,816	43,733	24,359	42,459	23,815	37,168	19,877
5.00	37,496	16,832	34,019	15,091	36,175	15,479	34,367	15,091	34,544	16,785
7.00	47,611	22,996	42,957	22,071	45,265	22,393	48,464	24,751	43,105	21,945
8.00	53,303	20,991	49,423	21,484	49,071	20,335	46,618	18,009	50,693	21,970
Example No.:	6		7		8		9		10	
7.00	43,887	...	47,429	...	46,115	...	45,786	...	49,288	...
6.00	41,059	17,512	36,792	14,548	44,173	17,974	43,593	17,865	35,061	11,586
5.00	32,434	14,641	39,119	19,137	41,545	17,615	36,013	15,453	36,175	18,250
4.00	30,138	15,910	28,336	13,278	26,792	11,981	33,385	16,562	29,846	14,765
5.00	35,351	19,383	33,328	18,807	34,367	19,868	32,254	16,753	37,120	20,446
4.00	32,254	16,188	30,197	15,699	25,087	12,812	24,283	12,858	33,328	16,207
6.00	46,153	24,438	45,366	24,851	43,198	25,629	39,807	23,904	44,559	23,166
5.00	33,670	13,690	31,722	13,177	35,915	15,537	41,106	19,012	36,623	15,440
7.00	44,173	22,833	44,127	23,573	44,697	22,210	43,640	19,682	53,179	26,095
8.00	54,479	23,099	55,446	23,531	50,990	21,385	48,192	20,660	76,600	26,435

The Beverton and Holt and linear formula estimates of q and M are tabulated in Table XI. The results show 37% and 27% reductions in the variances of $\hat{q}$ and $\hat{M}$, respectively, when the linear formula is applied.

TABLE XI. Comparison of Beverton and Holt estimates and linear formulae estimates of the mortality rates. Data from Tables IX and X. True value of M = 0.20, and q has the average value of q = .10.

	Beverton and Holt estimates		Linear formulae estimates	
Example	$\hat{q}$	$\hat{M}$	$\hat{q}$	$\hat{M}$
1	.073	.354	.083	.298
2	.071	.334	.057	.413
3	.119	.091	.110	.140
4	.199	−.327	.149	−.052
5	−.008	.774	.053	.438
6	.092	.225	.075	.315
7	.122	.059	.065	.375
8	.127	.052	.052	.465
9	.054	.454	.084	.287
10	.155	−.094	.121	.088
Standard deviation of the estimates from the true value	.054	.243	.034	.177

APPLICATIONS

The new linear formula (16) has been applied to Georges Bank haddock data (Taylor, 1958), and Fry's Opeongo lake trout data (Fry, 1949). Results are tabulated in Table XII. The standard deviations are the familiar regression estimates. While they are not strictly applicable here, more refined techniques (such as approximate least-squares estimates) have not been considered worth while due to the large error component. Indeed, the 95% confidence

TABLE XII. Linear formulae estimates of q and M of Georges Bank haddock fishery (data from Taylor, 1958), and Lake Opeongo trout fishery (data from Fry, 1949) and corresponding standard deviations. In brackets we have given Taylor's estimates for the Georges Bank fishery and, Paloheimo's (1958, using Beverton and Holt method) for the Opeongo trout fishery.

Age groups	$\hat{q}$	$\hat{M}$	Standard deviation s_q	Standard deviation s_m
	Georges Bank haddock data			
III and IV	.162 (.102)	−.574 (−.170)	.058	.414
IV and V	.051 (.085)	.242 (.012)	.040	.317
V and VI	.100 (.082)	−.082 (.004)	.061	.427
	Lake Opeongo trout fishery			
IX and X	.050 (.047)	.339 (.374)	.030	.413

limits are so wide that it is questionable whether the estimates in Table XII have any practical value.

The Lake Opeongo trout fishery is a seasonal fishery, hence catch equation (4) or equations (5), (15) are not quite applicable since they have been developed by assuming a year-round fishery. To what extent the use of correct equations would change our results has not been studied. We also note that while the Georges Bank fishery is a year-round fishery, the catchability varies considerably from season to season. This variability may account for our poor estimates.

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The Copepods *Calanus glacialis* Jaschnov and *Calanus finmarchicus* (Gunnerus) in Canadian Arctic-Subarctic Waters[1]

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ABSTRACT

The literature on *Calanus finmarchicus* (Gunnerus) in arctic–subarctic Canada is reviewed, and the history of the 2-size-group phenomenon in the North Atlantic subarctic region is discussed. *Calanus glacialis* Jaschnov is briefly described, and compared with material from North America, the characters emphasized being size and the structure of the fifth legs. It is concluded that specimens from arctic and subarctic North America agree essentially with *C. glacialis*, those from the subarctic and north boreal regions with *C. finmarchicus*. Occurrence of the 2 species in northern North America is given, that of the large *glacialis* alone being shown to coincide closely with the known extent of unmixed polar water, of the 2 together to occupy the region of mixed polar and Atlantic water, and of the small *finmarchicus* alone to inhabit Atlantic water.

INTRODUCTION

The copepod *Calanus finmarchicus* has long been considered as one of the most abundant and most important planktonic species in all northern seas. Wilson (1932, p. 23) referred to the distribution of the species as: "Everywhere in all the oceans, including the Arctic and Antarctic. . . ." Ekman (1953) included it among the cold-water cosmopolites. Marshall and Orr (1955) listed many of the widely spread points of occurrence, and gave for it a temperature range of −2 to 22°C and a salinity range of 29 to 35‰. Northern waters however have provided the bulk of the material on the species, and a very large number of publications deal with *Calanus finmarchicus* of the North Atlantic and more northerly subarctic and polar waters. In 1955, Jaschnov described a new species, *Calanus glacialis*, from north Russian seas. Acceptance of this necessarily upsets the well established distributional picture of *C. finmarchicus* which *C. glacialis*, according to its author, replaces in arctic waters.

The considerable material on marine benthos brought to light by nineteenth-century explorers in the Canadian north did not extend to the smaller plankters, which were largely ignored until near the end of the century. One of the first references to *C. finmarchicus* is in Rodger's (1894) account of the marine fauna from off northeast Baffin Island. Although comparatively few references have followed, they have covered wide regions of both eastern and western waters of

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northern Canada, and include Sars (1909), Willey (1920, 1923, 1931), Wilson (1936), Vibe (1950) and Johnson (1956). While these were concerned only with the occurrence of the species, 2 more recent works (Fontaine, 1955; Grainger, 1959) considered the biology of the species from Ungava Bay and Foxe Basin, respectively.

Early in the history of *C. finmarchicus* investigations the great length range of adults found in northern waters was noticed. Sars (1886) reported specimens from Jan Mayen of more than twice the size of the normal forms. In the Norwegian Sea, Gran (1902) noticed larger individuals in the north than in the south, and south of the Gulf of St. Lawrence, Willey (1919) reported a similar situation, the largest individuals being taken from the coldest waters. Currie (1918) found notably large specimens in the Bay of Fundy, and Willey (1920) only large individuals in and just east of the Beaufort Sea. Comments on the extreme size range from off West Greenland by With (1915) were followed by the recording by Størmer (1929) of 2 size groups of both adult females and stage V in the same area, the larger group described as occurring in northern cold, the smaller one in southern warm water. Jespersen (1934) expanded on the 2-group study, using females only, and showed the greatest proportion of large individuals in the north and west parts of Baffin Bay and along the coasts of Baffin Island and Labrador. He concluded that the large form was definitely associated with cold water. The demonstration of 2 size groups also was made from north of Spitzbergen by Farran (1936), and from East Greenland by Ussing (1938) and Jespersen (1939), the latter pointing out that large individuals were particularly numerous in deep (cold) water, smaller ones in surface (warmer) water. From north Foxe Basin, within the true arctic region of Canada, however, only large individuals, with no evidence of 2 size groups, were reported by Grainger (1959). It is perhaps significant that all the regions in which either great length variation or 2 length groups have been described fall either in or close to the subarctic marine area, as defined by Dunbar (1951), and that locations in which there is no evidence of either excessive length range or the 2-size-group phenomenon lie outside this area, both to the south and to the north.

Using material collected chiefly in the north Russian seas and data on length measurements from the literature, Jaschnov (1955) reviewed the *Calanus finmarchicus* problem and established as a result the new species named *C. glacialis* for members of the group previously recorded as "large" *finmarchicus*. Former "small" *finmarchicus* were retained as *C. finmarchicus* s.s. *C. glacialis* was designated the arctic form, and was listed as occurring in the Polar Sea, all Siberian seas, northern Barents Sea, cold waters of the Greenland Sea, White Sea and all the eastern Russian seas. *C. finmarchicus* s.s. was called a boreal species, occurring in the southern Barents Sea, off Norway, in the North Sea and over the North Atlantic.

Separation of the species was made on morphological grounds. Females of *C. glacialis* were given a total length range of 4.3 to 5.5 mm (cephalothoracic length therefore about 3.4 to 4.3 mm), and a ratio of body width to length of usually 1:2.7 to 1:3. The fifth legs were characterized by having along the inner

margin of their first segment a conspicuous concavity and large blunt teeth. The total length range of males was given as 4.7 to 5.2 mm (about 3.7 to 4.0 mm cephalothoracic length), and the fifth leg characterized by the relatively short endopodite not reaching farther than the middle of the second segment of the exopodite. In stage V, 3.2 to 4.7 mm total length (about 2.6 to 3.7 mm cephalothoracic length), the inner margins of the first segments of the fifth legs were described as showing clear concavities.

C. finmarchicus s.s. was described according to Sars (1901). Compared with *glacialis*, total length of females was given as 3.0 to 4.1 mm (cephalothoracic length therefore about 2.4 to 3.2 mm), and the ratio of body width to length as usually 1:3 to 1:3.5. The fifth legs were described as having the inner margin of their first segment either straight or very slightly concave, but not having the sharp inward curve of *glacialis*. The total length of males was given as 3.3 to 3.9 mm (cephalothoracic length about 2.6 to 3.0 mm), and the fifth legs characterized by the relatively long endopodite reaching as far as the distal third of the second segment of the exopodite. In stage V, 2.8 to 3.4 mm total length (cephalothoracic length about 2.2 to 2.8 mm), the inner margins of the first segments of the fifth legs were described as being straight or nearly straight.

In a later paper, Jaschnov (1957) discussed in greater detail than before other morphological characters, and analysed fifth leg tooth and bristle counts of several *Calanus* species. In particular, variations in the curve of the inner edge of segment one of the fifth legs of *C. finmarchicus* females were discussed, and it was pointed out again that while the typical form is either straight or perhaps slightly convex, a variation from this in which there is a slight inward curve exists. In another paper, Jaschnov (1958) discussed the origin of the "superspecies *C. finmarchicus* s.l.", proposing the development of *glacialis* during glacial times, and supposing its Pliocene ancestor also to have given rise to *finmarchicus* s.s. Brodsky (1959) has also recognized *glacialis* as a distinct species, and presents a map (his fig. 5) showing the distribution of *glacialis*, *finmarchicus* and other *Calanus* species.

It is perhaps remarkable that interpretation of the Russian workers should differ to such a degree from that of Jespersen (1934), who apart from Jaschnov had probably the most suitable collection for this study, and who stated (p. 31): "The two size groups of *Calanus finmarchicus* found in the West Greenland waters are undoubtedly to be regarded only as a larger and as a smaller form of the same species. For the most minute investigation of the different characters has failed to reveal differences beyond that of size and the relative dimensions incident to it." Jespersen reported average counts of 34.8 teeth for small individuals and 34.4 teeth for large individuals. No reference was made to any difference in shape or size of the teeth in the 2 groups.

MATERIAL EXAMINED

Specimens of *Calanus* from artic and subarctic North America were obtained from several sources. The bulk of the material was from collections made from the M.V. *Calanus*, of the Fisheries Research Board of Canada, in the area between

Labrador, Hudson and James Bays, Foxe Basin and Cumberland Sound, Baffin Island. Many collections made from H.M.C.S. (later C.G.S.) *Labrador* among the islands of the Canadian archipelago and in Baffin Bay and Davis Strait were used as were collections made from the *Cancolim II* in the Beaufort Sea. Additional material was acquired from Ice Island T-3, north of the Canadian islands in the Arctic Ocean, from Pelly Bay, from the Labrador Sea, the Strait of Belle Isle and eastern Newfoundland, and from the Gulf of Maine. Several thousand specimens were included in the available material, measurements and morphological data being recorded for about 2000 individuals.

Length frequency histograms of a number of samples showed evidence of 2 size groups, of the majority of samples however of only a single group, either large or small. No single length was found to separate the large and small individuals over the whole area considered; instead there appeared to be a more or less consistent variation in the separating length related to geographical location.

In Fig. 1 are length frequency histograms of selected material measured, cephalothoracic length being given in micrometer units (0.126 mm). Collections from Ungava Bay show the most evident 2-group composition, the size groups being divided at 25 units (3.2 mm).

At the majority of locations only individuals of 25 units and greater length occurred, as shown on the left side and the upper right side of Fig. 1. In central Davis Strait, the Labrador Sea and the Strait of Belle Isle however there is shown a slightly greater mean length for the small group than was found in the other samples (lower right side of the figure). In a series of 5 collections extending from west Davis Strait (close to the Greenland coast) to near the northern tip of Labrador, there is a clear indication of increase in mean length of the small size group from the Greenland coast to central Davis Strait, and a nearly identical situation is shown in Jespersen's material taken along almost the same line, the largest of the small group occurring in central Davis Strait, the smallest near either coast. Jespersen's (1934) division between his 2 size groups was put at about 3.5 mm, apparently because only specimens from south Davis Strait were included in his fig. 5. Figure 2 here shows histograms from several of Jespersen's south central Davis Strait stations compared with his material from north Baffin Bay. In the former region the 2 size groups are seen to be divided at about 3.5 mm, in the latter at about 3.2 mm. Analysis of the 2 bimodal groups showed means of 38.5 and 52.6 units (2.96 and 4.05 mm) in Davis Strait, and 36.4 and 50.6 units (2.80 and 3.90 mm) in north Baffin Bay. Tests of significance of difference between means of the 2 small and the 2 large groups of both samples showed a high degree of probability (difference between means about 3 times gratere than 3 standard errors of the difference between means) of significant difference between the small groups and between the large groups in the 2 samples. That is, both the small and large groups were significantly larger in the more southerly and warmer Davis Strait than in the more northerly and colder north Baffin Bay.

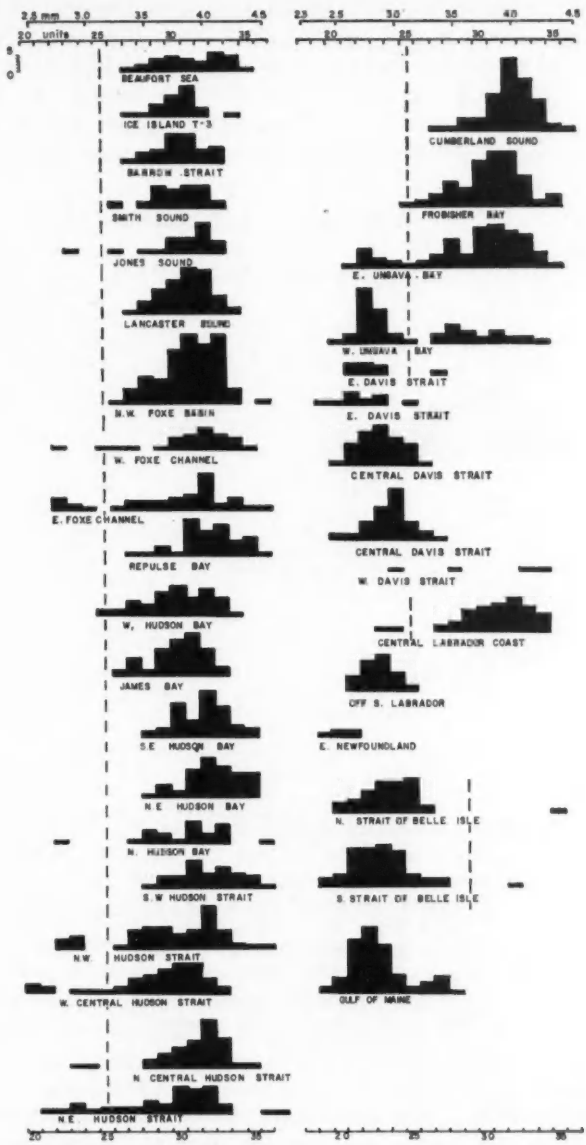

FIG. 1. Length frequency histograms of selected collections of females. Measurements are expressed in units of 0.126 mm. The vertical dashed lines show division between "large" and "small" individuals.

Of the morphological characters examined, emphasis was put on the structure of the fifth legs. From several hundred specimens examined for this character, the inner margin of the first segment of the fifth legs of 16 females between 2.4 and 4.4 mm long are shown in Fig. 3. Individuals from 2.4 to 3.2 mm long (top row in Fig. 3) and from 3.4 to 4.4 mm long (bottom row in Fig. 3) were selected as representatives of the small and large size groups respectively on the

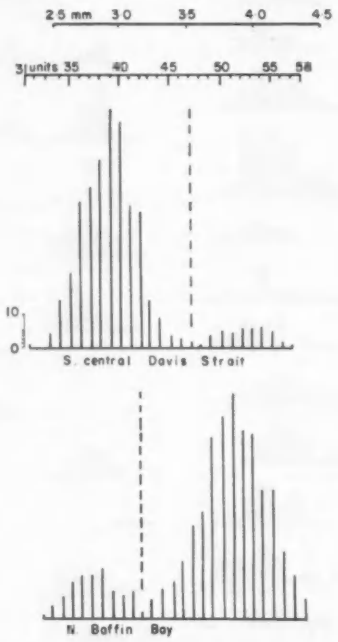

FIG. 2. Length frequency histograms of females from central Davis Strait and north Baffin Bay Godthaab stations (data from Jespersen, 1934). Lengths are given in units of 0.077 mm. The vertical dashed lines show division between "large" and "small" individuals.

basis of specimen length. Those from 3.2 to 3.4 mm long however are potentially representative of either length group on the basis of specimen length alone, depending on geographical location. Selection of illustrated representatives of this length range was made on the basis of length frequency of the whole collections from which single specimens originated, those from 3.2 to 3.4 mm in the top row of Fig. 3 being selected from collections the length frequencies of which showed

what was interpreted as the largest members of the small size group. Similarly, collections showing by their length frequency the smallest individuals of the large group were the source of individuals 3.2 to 3.4 mm long shown in the bottom row of Fig. 3.

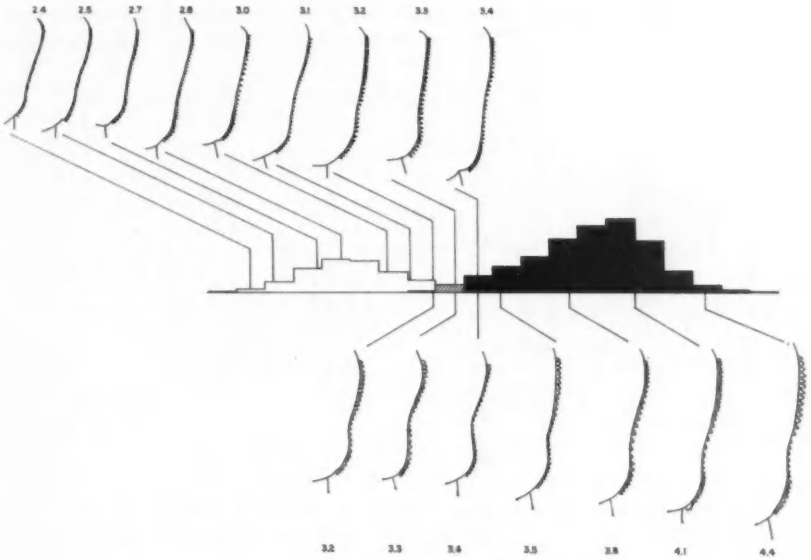

FIG. 3. First segment of the fifth legs of females.

Those of the top row resemble closely the various descriptions of *C. finmarchicus* available, in which the toothed margin is almost straight to slightly concave (Jaschnov, 1955, fig. 2; 1957, fig. 3). There is possibly a slight trend towards development of the inward curve from the smallest to the largest in this group; this trend is however by no means unvarying, for individuals up to the largest sometimes show the slightest deviation from a straight margin. Teeth tend to be relatively small and pointed. Among those shown in the bottom row, there is immediately apparent a more pronounced inward curve and larger, blunter teeth than in the small size group, with no suggestion of any trend of change in the curvature between the smallest and largest in this group. These specimens resemble the figures of *glacialis* in Jaschnov (1955), although the maximum inward curvature may be slightly less than shown by Jaschnov, being closer to the figure given by Brodsky (1959, fig. 3). Specimen length is not given for any of Jaschnov's or Brodsky's figures.

Males were few and sizes limited in available collections. Figure 4a, showing the left fifth leg of an individual 2.6 mm long, depicts *C. finmarchicus* according

to Sars (1909, pl. 3) and the description by Jaschnov (1955). Both this figure and that of Sars show the last segment of the endopodite reaching about two-thirds of the way along the penultimate segment of the exopodite, while in Jaschnov's figure the endopodite reaches almost to the distal end of the subterminal exopodite segment. Brodsky (1959) illustrates a structure intermediate

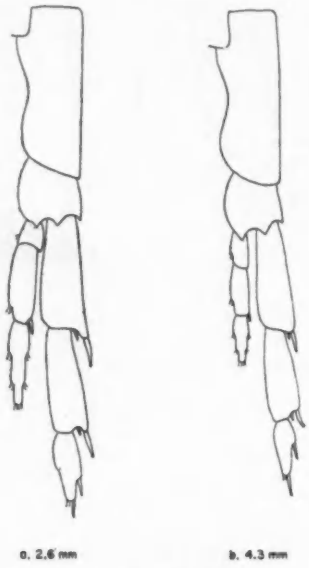

FIG. 4. Left fifth legs of males.

to Sars and Jaschnov. Figure 4b, the fifth left leg of a male 4.3 mm long, agrees with Jaschnov's description of *glacialis* but differs from his figure in having the last endopodite segment reaching about two-fifths of the way along the second last endopodite segment. There is obviously considerable variation in these structures, insufficient however to prevent inclusion of the specimens illustrated in *finmarchicus* (the smaller one) and in *glacialis* (the larger one).

Measurements were made of the ratio of body width to length throughout the size range. Figure 5 shows results of measurements made on 217 females from 2.4 to 4.5 mm long. The top solid line represents a width to length ratio of 1:3.5, the bottom solid line a ratio of 1:3.0, the dashed lines the approximate means of the 2 groups, the small one shown as open circles, the large one as dark circles. Most individuals (all but 2) of the small group fall within the range given by Jaschnov for *finmarchicus* (1:3 to 1:3.5). Most of the large group however also fall between 1:3 and 1:3.5 (Jaschnov's *glacialis* was given as 1:2.7 to 1:3); more than in the small group however are relatively broader, and about 20% of

these measured show a width-length ratio of less than 1:3. There is in general a relative widening of the cephalothorax with increase in its length in both groups, but among the largest of the small group there appears to be on the average a greater relative width than among the smallest of the large group. As far as practicable differentiation between the 2 groups is concerned, this criterion appears to have statistical value only, and not to serve as a basis for placing individual copepods within one group or the other.

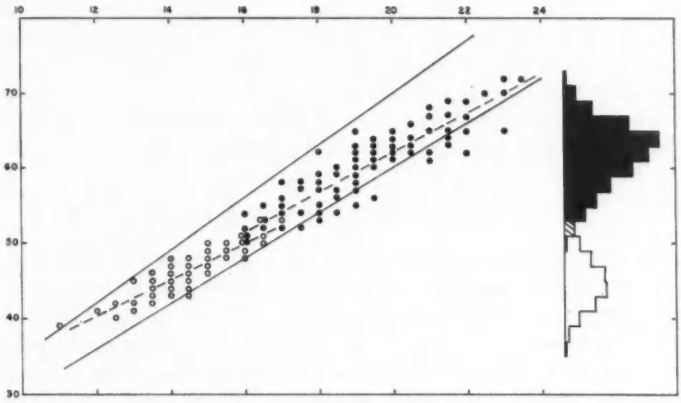

FIG. 5. Ratio of body width to length in units of 0.063 mm. The upper line shows a width to length ratio of 1:3.5, the lower line a ratio of 1:3.0.

Jaschnov (1957) presented data on the number of spines on the outer edge of the terminal endopodite segment of the fifth legs of females. Of 100 specimens of *finmarchicus*, 71% were reported to have only one spine, 25% 2 spines and 4% one and two (on different legs). Of 100 *glacialis*, 41% had one spine, 39% had 2 spines and 20% had 1 and 2 spines. Seventy specimens from both size groups were investigated here in this way, and data are given in Table I. In all, 70% have only 1 spine per leg, and there appears to be a clear and regular trend towards

TABLE I. Number of spines on the outer edge of the last endopodite segment of the fifth leg of females.

Cephalothoracic length (units)	Individuals with 1 spine	Individuals with 2 spines
20	8	2
22	8	2
25	7	3
27	8	2
30	6	4
32	7	3
35	5	5

fewer individuals with only 1 spine among the larger animals, varying from the order of 80% in the smallest to the order of 50% in the largest. There appears to be no sharp distinction on this basis between the two.

On the basis of size and structural differences discussed above, it is concluded that there is a consistent distinction between members of the so-called large and small size groups of *Calanus* in the area considered here; size difference serves in the majority of instances to distinguish members of one from the other, but within the size range shown to be common to both groups, in different parts of their range, individuals may be placed with reasonable certainty into either one or the other of the groups on the basis of fifth leg structure. Because of the degree and apparent consistency of this distinction, it is suggested that the large group be referred to *Calanus glacialis* Jaschnov, the small group to *Calanus finmarchicus* (Gunnerus), and that former records of *C. finmarchicus* from much of the arctic area of North America be considered as referring to *C. glacialis*.

ZOOGEOGRAPHICAL FEATURES

Locations of collections used in this work are shown in Fig. 6 as circles. Squares in the figure represent some of the Godthaab stations reported by Jespersen (1934) and other collections (Currie, 1918; Willey, 1919). Arrows indicate principal water movements. Dark circles are stations where only *glacialis* were found, and show exclusive occurrence of this species in the Beaufort and Polar Seas, among the islands of the arctic archipelago east to Smith Sound and eastern Lancaster Sound, south to southwest Foxe Basin, Hudson and James Bays, and along east Baffin Island south to Frobisher Bay. Half-dark and quarter-dark circles represent mixed collections of both *glacialis* and *finmarchicus* which extend from south Foxe Basin and north Hudson Bay through Hudson Strait and Ungava Bay, and from as far north as eastern Jones Sound southward to at least the Gulf of Maine. Quarter-dark and half-dark squares symbolize the same ratios of the 2 species, and show mixed populations as far north as Smith Sound with, at least in the north, relatively greater numbers of *glacialis* in west than in east Baffin Bay. White symbols represent occurrence of *finmarchicus* only, and are limited largely to central Davis Strait, being found also in the Gulf of St. Lawrence, south of Newfoundland and Nova Scotia and in the Gulf of Maine. Occurrence of *glacialis* south of Newfoundland and Nova Scotia (from Willey, 1919) may be seen at the northern colder stations only, locations farther offshore showing *finmarchicus* only. Collections considered from the southernmost part of the area treated here are few and do not necessarily show the southernmost limit of *glacialis*. It does seem probable however that south of Labrador *glacialis* is comparatively rare, and that its occurrence may be limited by the southernmost extension of subarctic water. Precise definition of its southern range would be of great value.

Occurrence of the 2 species obviously coincides to a considerable degree with water movements. Unmixed polar water flowing southward and southeastward

FIG. 6. Distribution of *Calanus glacialis* and *C. finmarchicus* in northern North America. Circles indicate collections first reported here, squares collections described by others (mostly Jespersen, 1934). Arrows denote principal water movements.

from the Arctic Ocean appears to support exclusively *glacialis* as unmixed Atlantic water to the south evidently contains only *finmarchicus*. The most northerly and westerly representatives of *finmarchicus* were found in south Smith Sound, east Jones Sound, south Foxe Basin and immediately south of Southampton Island, all of which receive warm currents with Atlantic influence. In Baffin Bay and Davis Strait, except at the strongly arctic near-shore station off south Greenland, Jespersen's data show a definite preponderance of *glacialis* on the arctic Canadian side, of *finmarchicus* on the more mixed Greenland side. It appears that exclusive occurrence of each of the 2 species, in polar and in boreal water, is separated by a combination of the 2 in the intermediate subarctic or mixed polar and Atlantic water, and that the degree of mixing may possibly be reflected by the ratio of *glacialis* to *finmarchicus*.

Brodsky (1959, fig. 5) shows on a map the general distribution of *C. glacialis* and *C. finmarchicus*, along with other species of *Calanus*. The line separating the 2 forms falls generally within the subarctic region as shown by Dunbar (1954, fig. 38), except for the northern part of the Sea of Okhotsk. Thus, except for the Sea of Okhotsk population, which may be a relict one, *glacialis* is shown by Brodsky to be a circumpolar arctic form, *finmarchicus* s.s. to be adjacent to it in the North Atlantic. While Brodsky did not show any region of mixture of the 2 forms, it is possible that the subarctic area may be defined, at least north of the Atlantic, by the occurrence of *Calanus glacialis* and *Calanus finmarchicus* together.

THE RELATION BETWEEN LATITUDE AND SIZE

The condition of poikilothermous animals in higher latitudes reaching greater size and greater age, as a result of slower growth, is widely known, and has been a readily available explanation for the presence of large *finmarchicus* in cold waters, small ones in warm waters. Marshall and Orr (1957), for example, concluded of *finmarchicus* that, apart from size variation associated with time of development within a year, the largest individuals were found in the coldest, the smallest in the warmest part of the range.

Considering the "small form" (*finmarchicus*), by itself, Clarke and Zinn (1937) found off Woods Hole a length range over the year of about 2.10 to 3.10 mm, and a range of mean values of about 2.30 to 2.75 mm, the greatest length occurring in March, the smallest in summer. Similar figures, although with variations in the times of maximum and minimum lengths, come from various workers in the British Isles. In the present material, the mean length of the Gulf of Maine sample is 2.80 mm (range 2.38 to 3.13 mm); the collection was made in April, probably near the time of greatest length. Means of 2.86 and 2.94 mm from the Strait of Belle Isle (range 2.38 to 3.38 mm) were obtained from late September collections. Similar means (2.86 and 2.94 mm) were recorded from southeast Davis Strait. In central Davis Strait a mean of 2.96 mm (range 2.50 to 3.38 mm) was found near mid-August, and a still larger size was found in the Godthaab material (Jespersen, 1934) from near the same location in mid-June, where the

mean was 3.08 mm (range 2.54 to 3.39 mm). Farther into arctic waters, mean values are lower: Ungava Bay, 2.86 mm (range 2.63 to 3.13 mm), and 2.84 mm (range 2.50 to 3.13 mm); north Baffin Bay (from Jespersen, 1934), mean 2.80 mm (range 2.46 to 3.23 mm). Overall range of mean lengths considered here is 0.33 mm, a figure smaller than the 0.45 mm total yearly range of means from off Woods Hole. But this overall range is much greater than the maximum difference (0.12 mm) between mid-June and mid-August apparent in central Davis Strait, and probably considerably greater than the seasonal range at any one location in the area considered here. There is therefore evidence to indicate an increase in length from the south at least part way to the northern limit in *finmarchicus*, and that maximum size is reached in the intermediate portion and not necessarily in the northernmost (or most arctic) part of the range.

Something similar is suggested from the available data on the large *glacialis*. The greatest mean length (3.98 mm; maximum 4.66 mm) was found in what may be called the intermediate area of Foxe Basin, Hudson Strait and north Hudson Bay, with smaller individuals taken in the Arctic Ocean and high-arctic archipelago (mean 3.83 mm; maximum 4.28 mm) and in Baffin Bay, Davis Strait and more southerly regions (mean 3.87 mm; maximum 4.41 mm). These data are in keeping with Jespersen's (1934) maximum length west of Greenland of less than 4.5 mm and Huntsman's (1919) maximum length in the Newfoundland-Nova Scotia region of about 4.4 mm. The greatest length found in a small sample, taken in winter, from the Gulf of Maine was only 3.59 mm, the mean length of 10 individuals 3.39 mm. It may be pointed out too that north European and Asian collections (Jaschnov, 1955) show the largest individuals from the Barents and White Seas, with smaller specimens reported from the more arctic Polar, Kara and Greenland Seas, as well as in the more southerly Seas of Okhotsk and Japan.

There appears to be in both *finmarchicus* and *glacialis* variation in length latitudinally over their range. The smallest individuals develop in the southern (warmest) parts, the largest intermediate to the north-south limits of distribution, and, it is suggested, smaller sized individuals towards the northern (coldest) extremities. While the ranges of both are in large part separate, there is an appreciably large area of overlap in which the largest individuals of both appear. Data suggest however that the largest individuals of both *finmarchicus* and *glacialis* do not develop together, but rather that the largest *glacialis* occur farther north (in colder, more arctic water) than the largest *finmarchicus*. This, if correct, would imply that the coldest waters do not necessarily produce the largest individuals of either species, and that both have optimum and slightly differing environmental conditions under which maximum size is attained. It seems from this that the tendency toward development of greater size with decreasing temperature may be checked in the lowest temperature range by a factor or factors which in some way inhibit further size increase. The possibility of this being food supply can be only conjecture with our present knowledge of high arctic conditions. It may be stated however that available food for *C. glacialis* in the northern and western parts of the arctic archipelago appears to be in far shorter supply than in the regions of Foxe Basin, North Hudson Bay and Hudson

Strait, or off east Baffin Island. Increase in size achieved with decreasing temperature may prevail as long as food supply remains adequate. With further decrease in temperature (that is, farther into the arctic), reduced food supply may inhibit additional increase in size and possibly result in a decrease in maximum size attained.

YOUNGER STAGES

So far, separation of *glacialis* and *finmarchicus* has been made primarily between adult females. In adult males and in stage V copepodites, fifth leg structure appears to be a valid criterion of difference between the two, and in the latter at least a clear length distinction has been shown. In collections such as Digby's (1954) from East Greenland (referred to *C. finmarchicus* only), 2 length groups are apparent in stage IV, suggesting, as in stages V and VI from the same area, the presence of both species. No structural differences however have been shown between the 2 size groups in this stage. There has not been shown any clear indication of bimodality in length distribution of stages younger than stage IV. However, comparison of Digby's East Greenland data, which from length ranges may have included both species although all were called *finmarchicus*, and Grainger's (1959) Foxe Basin data, which evidently included only *glacialis*, suggests a possible length difference in the younger stages. Similar maximum lengths are shown in all stages from VI to II, and minimum lengths in stages VI and IV in Foxe Basin are almost identical with minimum lengths of the large size group in the same stages in East Greenland. Minimum lengths in stages III and II in Foxe Basin however fall close to the median lengths of the same stages in East Greenland. Larger mean lengths therefore for stages II and III were found in Foxe Basin than in Greenland, the Foxe Basin length range approximating the upper half of the length range in both stages in East Greenland. At a much younger level, the possibility of distinguishing between the eggs of *finmarchicus* and *glacialis* comes from observations of Marshall *et al.* (1953) who reported a form from Trømso, Norway, which according to Jaschnov (1957) may be *C. glacialis*.

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Comparative Osteology of Representative Salmonid Fishes, with Particular Reference to the Grayling (*Thymallus arcticus*) and its Phylogeny[1,2]

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ABSTRACT

The purpose of this study is to describe the morphology, particularly the osteology, of the grayling (*Thymallus arcticus*), in relation to that of the other salmonid fishes, in order to assess the phylogenetic position of the grayling and to synthesize the natural classification of the Salmonidae.

Fresh and preserved material of 33 species in 9 genera of Salmonidae were studied. The study materials included dried whole skeletons from fresh fishes, stained bones of preserved specimens, and cross sections of larval stages. Effort was made to eliminate bias due to ontogenetic and sexual differences.

The Salmonidae are soft-rayed teleost fishes belonging to the suborder Salmonoidei of the generalized order Clupeiformes (Isospondyli). Prior classifications of the salmonids have arranged them into one, two, or three families. As herein visualized, the family Salmonidae contains those salmonoid fishes that have three upturned caudal vertebrae. They are divided into three subfamilies: Salmoninae, the trouts and salmons, with an orbitosphenoid bone and a suprapreopercular bone, a basibranchial plate, teeth on the maxilla, no dermosphenotic bone, and parietals separate at the midline; Thymallinae, the graylings, with no orbitosphenoid, suprapreopercle or basibranchial plate, a dermosphenotic bone, teeth on the maxilla, and parietals meeting at the midline; and Coregoninae, with orbitosphenoid and dermosephnotic bones, no suprapreopercle, no teeth on the maxilla, and parietals meeting at the midline.

The grayling possesses only two invariable morphological differences from other salmonids. These are the absence of an orbitosphenoid bone and the presence of seventeen or more dorsal fin rays. In other characters, there is overlap with one or the other subfamilies.

Three osteological characteristics are thought to be more fundamental than the others: the toothless maxilla in the Coregoninae, the lack of an orbitosphenoid in the Thymallinae, and the separation of the parietals by the supraoccipital in the Salmoninae. Each character is distinctive for only one subfamily, it being common to the other two. The complete bony and cartilaginous skeletal system of the grayling is illustrated, as are many osteological features of the trouts and whitefishes.

Within the subfamily Salmoninae, 5 genera (*Brachymystax*, *Hucho*, *Salvelinus*, *Salmo*, and *Oncorhynchus*) are recognized and defined. The Thymallinae consists of a single genus *Thymallus* with 4 species. Three genera of Coregoninae are recognized: *Prosopium*, *Coregonus*, and *Stenodus*. The discovery that *Prosopium* has a basibranchial plate, taken together with previously known characters, justifies recognition of generic rank for this group. The group commonly ranked as a genus *Leucichthys* does not display enough difference to warrant such segregation and is synonymized with the genus *Coregonus*. *Stenodus* is found to have distinctive characters not heretofore noted and may rank as a genus separable from but related to *Coregonus*.

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INTRODUCTION

THE GRAYLINGS are soft rayed teleost fishes belonging to the suborder Salmonoidei of the generalized order Clupeiformes (Isospondyli). They are most closely allied to the trouts and whitefishes, and some authors (Boulenger, 1895; Regan, 1914) have assigned all three groups to the family Salmonidae. Others (Jordan and Evermann, 1896; Tchernavin, 1923; Berg, 1940, 1955) have placed the graylings in a separate family, the Thymallidae. Since the literature is incomplete regarding the osteology of the grayling, this study was undertaken to advance our knowledge of fish morphology. Comparisons with other salmonoid fishes were made in order to clarify the phylogenetic position of the grayling and to place the classification of the Salmonidae on a firmer foundation.

Berg (1940) listed 11 families among the Salmonoidei, but revisions by Chapman (Plecoglossidae, 1941a; Osmeridae, 1941b; Argentinidae, 1942; Microstomidae, 1948) and recent lumping of several bathypelagic families from the suborders Opisthoproctoidei and Salmonoidei into the Argentinidae (Hubbs, 1953) have reduced this number to about seven. The Salmonoidei are characterized by the presence, usually, of an adipose fin, ribs inserted on autogenous parapophyses, the neural and haemal arches of the caudal fin skeleton are laterally compressed, and oviducts absent or incomplete (Regan, 1913; Gosline, 1960). The salmonines (trouts), coregonines (whitefishes), and thymallines (graylings) are separable from the other salmonoid fishes by the three upturned vertebrae in the caudal fin (Regan, 1914). They have been variously placed in one, two or three families, but that the three groups constitute a monophyletic assemblage seems generally agreed. This assemblage is here regarded as a family, Salmonidae, and the three included groups are treated as subfamilies: trouts, Salmoninae; whitefishes, Coregoninae; and graylings, Thymallinae.

The graylings consist of a single genus *Thymallus* composed of 4 species, as revised by Svetovidov (1936). *Thymallus brevirostris* Kessler (*Phylogephyra* Boulenger) has larger teeth than the other 3 species and the articulation of the lower jaw is situated behind the posterior margin of the eye. It has a very restricted range in northwest Mongolia. *Thymallus thymallus* (Linnaeus) has less well developed teeth than does *T. arcticus* and the maxilla does not extend beyond the anterior margin of the eye. It is found in the British Isles and across northern and central Europe. *Thymallus nigrescens* Dorogostajskij is similar to *T. arcticus* but it has more gill rakers (26 to 33 as compared with 14 to 22 in *T. arcticus*). It is restricted to Lake Kosogol in Mongolia (Svetovidov, 1936). *Thymallus arcticus* has the widest distribution of the four, occurring from western Siberia across northern Asia into North America. In North America there once lived 3 (possibly 4) isolated stocks of *Thymallis arcticus*. The most widely distributed of these, named *Thymallus signifer* by Richardson (1823), occurs in Alaska and northern Canada. *Thymallus montanus* (Milner, 1874) was described from mountain streams of the upper Missouri drainage. *Thymallus tricolor* (Cope, 1865) a now extinct geographic stock, was once abundant in the streams of northern Michigan along the upper Great Lakes. A possible fourth colony

may have been native to Lake Ontario, whence came two museum specimens, the types of *Thymallus ontariensis* Valenciennes (see Jordan and Evermann, 1896: 518; Bertin, 1940: 306).

American workers have classified these several stocks variously as distinct species, as subspecies of a single species, or as comprising two species, one with two subspecies. Walters (1953, 1955) treated the American grayling, *Thymallus signifer*, as conspecific with the Asiatic species, *Thymallus arcticus* (Pallas), and relegated the American forms to subspecific status without giving characters for the latter. Whether or not the 4 geographic stocks of American graylings are sufficiently distinct to merit separation into subspecies is uncertain. A careful comparison of the forms is needed, but this is beyond the scope of the present inquiry.

Both the European grayling, *Thymallus thymallus* (Linnaeus), 1758, and the eastern Siberian form, *Thymallus arcticus* (Pallas), 1793, were originally described in *Salmo*. Richardson, in describing the North American form *signifer* (1823), placed it in the genus *Coregonus*. *Thymallus* (proposed by Cuvier, 1829) was separated from *Salmo* on the basis of the small mouth and teeth, less deeply cleft jaws, long and high dorsal fin, and larger scales. The coregonine fishes were separated from the salmonine fishes by Cope (1871, 1872) chiefly because the parietal bones meet at the midline in the coregonines, and are separated by the supraoccipital bone in the salmonines. Gill (1893, 1895) disputed the work of Cope and stated (incorrectly) that in the coregonines the parietals are also separated by the supraoccipital. This left *Thymallus* as the only genus with parietals in contact, and as a result, Gill created the family Thymallidae, using the long dorsal fin and the presence of epipleural spines on the anterior ribs as supporting evidence for the action. The coregonines were relegated to subfamily status within the Salmonidae. Boulonger (1895) called attention to Gill's erroneus observation on the parietal separation in the whitefishes. He pointed out that all salmonoid fishes have epipleural spines and that the development of the dorsal fin is too trivial to be used as a family character. Consequently he saw no sound evidence for separating either the thymallines or the coregonines from the Salmonidae. Jordan and Evermann (1896) retained Gill's classification and used the same diagnostic characters. In Regan's classification (1914) the Salmonidae was divided into two subfamilies, the Salmoninae, with stronger dentition, separated parietals and smaller scales, and the Coregoninae. *Thymallus* was assigned to the Coregoninae, because it has weak dentition, parietals meeting at the midline, and large scales. Kendall (1935: 8) stated that *Thymallus* is not a link between the coregonines and salmonines and that the ensemble of characters of both *Thymallus* and *Stenodus* is more than generically distinct. Tchernavin (1923; 1939) recognized the graylings as a separate family, closely related to the Salmonidae, but without an orbitosphenoid bone. He further distinguished the Thymallidae from the Osmeridae by the absence of teeth on the mesopterygoid bone. In the recent classification by Berg (1940, 1955) the graylings were again placed in a separate family, Thymallidae, because of the lack of an orbitosphenoid, the presence of three tabulars on each side, a hypethmoid bone, two supraorbitals,

and a long dorsal fin. The salmonines and coregonines were ranked as subfamilies of the Salmonidae.

An abundant literature has appeared on the embryology and osteology of the Salmoninae, particularly *Salmo salar* Linnaeus and *Salmo trutta* Linnaeus. The early works date from Parker (1873), but the more recent osteological papers by de Beer (1927, 1937), Gregory (1933), Saunderson (1935), Holmgren and Stensiö (1936), and Tchernavin (1937, 1938a, 1938b) were particularly useful in this study. The coregonine fishes have received less extensive morphological study, although Price's (1934) work on the embryology of *Coregonus clupeaformis* (Mitchill) and Berg's (1940: 232–238) osteological material on *Coregonus lavaretus* (Linnaeus) and *Stenodus leucichthys* (Güldenstädt) have been helpful.

No complete account of the osteology of the grayling appears in the literature, although a number of diagnostic characters have been mentioned in conjunction with studies on other salmonoid fishes. This deficiency has resulted in some discrepancies and disagreement in regard to the morphology of the grayling and to its phylogenetic position.

The primary object of this work is an attempt to bridge the gap in our knowledge of the salmonoid fishes by presenting a description of the osteology of the grayling, *Thymallus arcticus* (Pallas). In addition, the phylogenetic position of the grayling is investigated through comparison with other salmonids and the classification of the Salmonidae is assessed.

At the taxonomic level at which this work was conducted, the skeleton appears to present the greatest promise for reliable comparison, and it has been stated (Tchernavin, 1937: 237) that "osteology offers a fairly safe guide to the natural arrangement of fishes." However, developmental stages and other morphological aspects have been studied to some extent.

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MATERIALS, METHODS AND TERMINOLOGY

Materials

The data on *Thymallus arcticus* were obtained from three sources: developmental stages, preserved specimens, and fresh adult fish. Developmental stages were collected from hatchery material by Mr A. E. Tangen of the Montana Department of Fish and Game. Specimens were collected at the time of hatching (total length 12.0 mm) and at 3-day intervals thereafter for 2 months (total length 34.5 mm). Twenty-two specimens (standard length 27.0 to 128.5 mm) were obtained from preserved material (UMMZ 167092, 169572, 169573, 169574, 169575) in the University of Michigan Museum of Zoology. These came from fish hatcheries in South Dakota, Wyoming, and Montana, or were collected in Alaska. Twelve mature adults in spawning condition (standard lengths 275.0 to 335.0 mm) were collected from Red Rock Creek, Beaverhead County, Montana by Dr C. J. D. Brown of Montana State College. These were frozen and were used for fresh osteological preparations (UMMZ 172465-S).

A substantial amount of fresh material was available for comparative study. When this was inadequate, preserved museum specimens were employed. Tables I, II and III itemize the material used, some merely for X-rays, some for extended study.

TABLE I. Specimens of Coregoninae used in the study.

Species	Number of specimens	Standard length	UMMZ number
	no.	*mm*	*No.*
Coregonus alpenae (Koelz)	2	120 to 140	172475-S
Coregonus artedii LeSueur	42	25 to 267	95649, 95650, 145300, 172466-S, 172467-S, 172471-S, 172472-S, 172473-S, 172474-S, 172480-S
Coregonus clupeaformis (Mitchill)	17	28 to 325	54314, 75323, 75324, 75327, 75332 to 75335, 81555, 162159
Coregonus hoyi (Gill)	13	75 to 205	52930, 54349, 172479-S
Coregonus kiyi (Koelz)	10	132 to 218	59415, 59438, 59439, 172477-S
Coregonus nasus (Pallas)	1	375	
Coregonus reighardi (Koelz)	4	191 to 211	172476-S
Coregonus sardinella Valenciennes	2	216 to 239	
Prosopium abyssicola (Snyder)	2	120 to 140	141811
Prosopium coulteri (Eigenmann and Eigenmann)	18	59 to 110	167953, 167954, 169058-S
Prosopium cylindraceum (Pallas)	12	31 to 297	52880, 59702, 59732, 59804, 68929, 141761, 167963
Prosopium gemmiferum (Snyder)	10	149 to 167	141809, 156788
Prosopium spilonotus (Snyder)	2	151 to 157	162330
Prosopium williamsoni (Girard)	6	53 to 147	140241, 161844
Stenodus leucichthys (Güldenstädt)	8	474 to 630	161995, 162455, 172387-S

TABLE II. Specimens of Salmoninae used in the study.

Species	Number of specimens	Standard length	UMMZ number
	no.	*mm*	*No.*
Brachymystax lenok (Pallas)	1	132	172490
Hucho hucho (Linnaeus)	1	493	177294
Hucho perryi (Brevoort)	1	284	172493
Oncorhynchus gorbuscha (Walbaum)	3	62 (2 adult heads)	147432, 172444-S
Oncorhynchus keta (Walbaum)	10	45 to 176	106275, 141105, 172452-S
Oncorhynchus kisutch (Walbaum)	5	38 to 58 (1 adult head)	93847
Oncorhynchus masou (Brevoort)	2	112 to 125	
Oncorhynchus nerka (Walbaum)	17	70 to 252 (7 adult heads)	117877, 144805, 166742, 167457, 172443-S, 172453-S, 172454-S
Oncorhynchus tshawytscha (Walbaum)	12	36 to 258 (1 adult head)	93867, 143188, 146364, 146365, 147328
Salmo clarki Richardson	5	167 to 239	136872, 167463
Salmo gairdneri Richardson	16	44 to 273	61837, 127601, 171042-S, 172468-S, 172469-S
Salmo ohridanus Steindachner	1	234	177293
Salmo salar Linnaeus	10	49 to 155	126538, 141019, 145562
Salmo trutta Linnaeus	18	19 to 413	1245553, 130641, 172470-S
Salvelinus fontinalis (Mitchill)	32	29 to 266	69641, 85467, 172462-S
Salvelinus malma (Walbaum)	3	(3 adult heads)	172458-S
Salvelinus namaycush (Walbaum)	32	22 to 653	81645, 162155, 172463-S, 172464-S, 172481-S to 172486-S

TABLE III. Other salmonoids used in the study.

Species	Number of specimens	Standard length	UMMZ number
OSMERIDAE	*no.*	*mm*	*No.*
Allosmerus attenuatus (Lockington)	4	46 to 75	60911, 93883
Hypomesus olidus (Pallas)	2	77 to 83	61245
Hypomesus pretiosus (Girard)	2	102 to 109	93887
Osmerus mordax (Mitchill)	23	42 to 187	72242, 172478-S
Spirinchus thaleichthys (Ayres)	2	80 to 97	60919
ARGENTINIDAE			
Argentina sialis Gilbert	2	88 to 103	94697, 94698
Argentina silus Ascanius	1	93	147278
PLECOGLOSSIDAE			
Plecoglossus altivelis Temminck and Schlegel	1	281	169000

Some observations were made on the Elopidae, Osmeridae, Argentinidae, and Plecoglossidae, especially to check statements made by other workers. Except for *Osmerus mordax*, all were based on preserved material.

All study material is preserved in the Museum of Zoology of the University of Michigan (UMMZ).

METHODS

Cross sections were made of the early stages (12 to 30 mm in total length) for *Thymallus arcticus*, *Coregonus artedii* and *Salmo trutta*. These were fixed in either Bouin's fluid or 10% formalin and stained with Harris's hematoxylin and eosin (Guyer, 1953). Preserved specimens were cleared in a solution of KOH and stained with alizarin red S for bone, or toluidine blue for cartilage, following the method prescribed by Evans (1948). Dried whole skeletons were prepared from fresh material by use of dermestid beetle larvae. Since cartilage occupies an important part of the skeleton of salmonoid fishes, dried preparations were unsuitable for some work. Therefore, some specimens were disarticulated for study after immersing the fresh fish briefly in hot water to loosen the flesh. The bones were later stained with alizarin red S and preserved in alcohol or glycerine. Gross anatomical dissections were made on both preserved and fresh material before skeletons were prepared. Where available specimens were few, additional vertebral counts were obtained from X-ray negatives of preserved specimens. In contrasting the osteology of different species, either specimens of comparable lengths or an equivalent stage of sexual maturity were employed.

In general, measurements and counts are adapted from Hubbs and Lagler (1947). All measurements were made in millimeters with dividers. The *total length* is the greatest dimension, in a straight line, from the anterior tip of the head to the posterior tip of the caudal fin. This measurement was used for developmental stages, before the vertebrae were ossified and while the caudal fin was heterocercal. The *standard length* is the greatest dimension, in a straight line, from the anterior tip of the upper lip to the hidden base of the caudal fin rays. All *rays* (rudimentary and principal) were counted in the dorsal, anal, and paired fins. In the dorsal and anal fins, the last ray is considered double at the base and is counted as one. The caudal fin ray count is the number of branched rays, plus two. The count of *gill rakers* is that of the first arch, with rudimentary rakers included. Unless otherwise stated, the *branchiostegal rays* counted includes all the branchiostegals on the left side. Three rays are usually borne on the epihyal and the remainder on the ceratohyal. The *pyloric caeca* include the tips of all the finger-like projections at the junction of the stomach and intestine. In making the count of *vertebrae*, each centrum was counted as one if it was separated on either side by a definite suture. Thus, the last three upturned vertebrae were counted as three. The precaudal vertebrae include all those that do not have a well-developed haemal spine. The rib, epineural, and epipleural count is an enumeration of all of these structures that are wholly or partially ossified.

Observations and measurements of skeletal elements, ova, and developmental stages were made with dividers under a dissecting binocular microscope. Illustrations were made from photographs and from drawings, using a compound microscope with a camera lucida.

TERMINOLOGY

The osteological terminology adopted is that most commonly accepted. Unless otherwise stated it agrees with Harrington (1955) for the skull, Stokely (1952) for the vertebral column, Starks (1930) for the pectoral girdle, and Regan (1910) for the caudal fin.

Abbreviations, definitions and synonyms of skeletal elements are as follows:

A. Angular, *os angulare* (dermarticular, Goodrich, 1930; articular, Gregory, 1933; de Beer, 1937; Berg, 1940). A pair of jaw bones which are both endochondral and intramembranous in origin, and which fit into the triangular notch of the dentaries, anteriorly and articulate posteriorly with the quadrates.

AC. Actinost, *os actinostum* (radial, Goodrich, 1930; Berg, 1940; Dineen and Stokely, 1954). The four small endochondral bones of each pectoral girdle which articulate proximally with the scapulae and distally with the fin rays.

AFR. Anal fin ray (lepidotrichia, Goodrich, 1930). The dermal rays, both rudimentary and principal, of the anal fin.

BB. Basibranchial, *os basibranchialium* (anterior copula, Tchernavin, 1938b; copulae, Ramaswami, 1952a, 1952b). A series of 4 unpaired endochondral bones forming the floor of the oral cavity. The first articulates anteriorly with the cartilaginous basihyal and the fourth articulates posteriorly with the cartilaginous basibranchial or posterior copula.

BH. Basihyal, *cartilago basihyalis* (lingual cartilage, Tchernavin, 1938b; glossohyal, Ridewood, 1904a; Chapman, 1942). A single cartilaginous component forming the base of the tongue.

BOC. Basioccipital, *os basioccipitale*. A median endochondral bone which forms the posterior floor of the cranial cavity and articulates with the first vertebra.

BP. Basibranchial plate, *os basibranchialium plattum* (supra-copula, Tchernavin, 1938b; suprabasal, Chapman, 1941a; dental cement bone, Chapman, 1941b). A median dermal ossification covering the basibranchials and often bearing basibranchial teeth, the so-called hyoid teeth. In some species two median bones are present.

BPTG. Basipterygium, *os basipterygium* (pelvic bones, Chapman, 1941a, 1941b). A pair of triangular endochondral bones which form the pelvic girdle.

BR. Branchiostegal ray, *os radii branchiostegi*. A paired series of flat dermal bones which lie below the interopercles and belong to the hyoid arch. The larger, posterior 3 rays articulate with the epihyal; the remainder articulate with the ceratohyal.

BS. Basisphenoid, *os basisphenoideum*. A small, median Y-shaped bone located in the rear of the orbit. The arms of the Y curve around the pituitary body and the leg bisects the posterior myodome and then meets the parasphenoid bone.

C. Centrum, *os centrum*. The spool-shaped portion of the vertebra which in embyrological development topographically displaces the notochord.

CB. Ceratobranchial, *os ceratobranchialium*. A pair of long endochondral bones present in each of the five paired gill arches which articulate with the epibranchials, dorsally, and the hypobranchials, ventrally.

CC. Coracoid, *os coracoideum*. A pair of triangular endochondral bones of the pectoral girdle which articulate with the cleithra and the scapulae.

CH. Ceratohyal, *os ceratohyale*. The ceratohyals are a pair of flat endochondral bones which belong to the hyoid arch. They articulate anteriorly with the hypohyals and posteriorly with the epihyals. Each ceratohyal bears from 6 to 10 branchiostegal rays.

CL. Cleithrum, *os cleithrum*. A pair of large, curved intramembranous bones which form an extensive part of the pectoral girdle.

CM. Coronomeckelian, *os coronomeckelium* (sesamoid articular, Ridewood, 1904a; *os Meckeli*, Berg, 1940; sesamoid angular, Ramaswami, 1952a, 1952b). A pair of bones which are believed to be an intramembranous ossification on the mesial surface of the angulars.

D. Dentary, *os dentale*. A pair of large, toothed, mixed bones of the lower jaw.

DF. Dorsal fontanelle (temporal foramen, Berg, 1940). A pair of circular openings in the cartilaginous roof of the chondrocranium.

DS. Dermosphenotic, *os dermosphenoticum*. The pair of small, dermal postorbital bones which bear triradiate sensory canals. They are absent in the Salmoninae.

E. Epural, *os epurale*. Two or three, median endochondral bones which lie dorsal of the uroneurals in the caudal fin skeleton. They are detached from the uroneurals and are believed to be modified neural spines.

EB. Epibranchial, *os epibranchialium*. Four pairs of endochondral bones, one in each of the first four gill arches. They articulate, dorsally, with the pharyngobranchials and, ventrally, with the ceratobranchials.

ECT. Ectopterygoid, *os ectopterygoideum* (pterygoid, Chapman, 1941a, 1941b, 1942; Dineen and Stokely, 1954). A pair of thin, splint-like dermal bones which lie on either side of the palate, between the palatine and quadrate bones.

EH. Epihyal, *os epihyale*. A pair of rounded endochondral bones which belong to the hyoid arch. They articulate anteriorly with the ceratohyals and dorsally with the interhyals, and bear three pairs of branchiostegal rays.

EHS. Expanded haemal spine. The transverse processes of the caudal vertebrae become fused and form posteroventrally directed projections. The projections belonging to the last 7 or 8 vertebrae are broad and flat, and are called expanded haemal spines.

EN. Epineural, *os epineuralium* (epipleural, Goodrich, 1930). A series of small, paired intermuscular bones of the axial skeleton which articulate with the anterior neural arches and point posterodorsally.

ENS. Expanded neural spine. A series of ossifications which extend dorsad around the spinal cord and form neural arches. The posterior arches fuse to form spines which project dorsocaudally. The last 7 or 8 of the series are broad and flat, and are called expanded neural spines.

EOC. Exoccipital, *os exoccipitale* (lateral occipital, Berg, 1940). The pair of endochondral bones which form in the posterior wall of the chondrocranium and partially surround the foramen magnum.

EP. Epipleural, *os epipleuralium*. A paired series of short ribs which project caudally into the myocommata from the bases of the pleural ribs.

EPO. Epiotic, *os epioticum*. A pair of endochondral bones which form in the posterodorsal surface of the chondrocranium and enclose the posterior semicircular canals.

ES. Extrascapular, *os extrascapulare* (scalebone, Gregory, 1933; tabular, Berg, 1940; supratemporal, Chapman, 1941a, Ramaswami, 1952b). A transverse series of from 4 to 10 dermal bones which lie behind the parietals and enclose the supratemporal sensory canal.

F. Frontal, *os frontale*. A pair of flat, triangular dermal bones which cover most of the dorsal surface of the chondrocranium.

FM. Foramen magnum, *foramen magnum*. The posterior opening in the chrondrocranium, through which the spinal cord passes as it leaves the brain.

H. Hypural, *os hypuralium*. A series of 7 expanded haemal spines in the caudal fin which lie ventrally of the three upturned vertebrae and the urostyle.

HA. Haemal arch. A bridge of bone formed by an elongation of the transverse processes around the caudal artery and vein; present in a few precaudal and most caudal vertebrae.

HB. Hypobranchial, *os hypobranchialium*. A pair of endochondral bones present in each of the first three gill arches. They articulate dorsally with the ceratobranchials and ventrally with the basibranchials.

HE. Hypethmoid, *os hypethmoideum* (mesethmoid, Gregory, 1933; de Beer, 1937; ethmoid, Harrington, 1955). A median endochondral ossification which lies between the nasal capsules. Hypethmoid (Berg, 1940) is used to avoid confusion with the ethmoid cartilage and the supraethmoid bone.

HH. Hypohyal, *os hypohyale*. A pair of upper and lower, cone-shaped endochondral bones of the hyoid arch that connect the ceratohyals with the median basihyal.

HS Haemal spine (haemal process, Berg, 1940). The posteriorly directed ventral projections formed by elongation and fusion of the transverse processes. Vertebrae which bear haemal spines are designated as caudal vertebrae.

HY. Hyomandibular, *os hyomandibulare*. A pair of hatchet-shaped endochondral bones which suspend the lower jaw from the cranium.

IH. Interhyal, *os interhyale*. A pair of small, cylindrical endochondral bones which connect the epihyals with the symplectic and hyomandibular bones.

IN. Interneural, *os interneuralium* (dorsospinalia, Berg, 1940). A series of median supporting rods which lie in the muscle anterior of the dorsal fin, between the bifurcated neural spines.

IO. Infraorbital, *os infraorbitalium* (jugal, Gregory, 1933; suborbital, Chapman, 1941a; Vladykov, 1954; Harrington, 1955). One pair of small dermal bones which lie between the lachrymals and the first pair of postorbitals.

IOP. Interopercle, *os interoperculum*. A pair of thin, triangular dermal bones which lie below the preopercles, separating them from the subopercles.

LA. Lachrymal, *os lacrimale* (lacrimal, Allis, 1897; praeorbital, Berg, 1940; suborbital, Vladykov, 1954). A pair of small dermal bones which form the lower anterior rim of the orbits and contain the termini of the infraorbital canals.

LP. Lingual plate, *os linguale plattum* (dermentoglossum, de Beer, 1937; supralingual bone, Tchernavin, 1938b; Vladykov, 1954; dental cement bone, Chapman 1941a, 1942). A median dermal ossification which covers the cartilaginous basihyal and bears the "tongue teeth".

M. Maxilla, *os maxillare*. The pair of dermal bones of the upper jaw which articulate anteriorly with the premaxilla but are without a posterior articulation. They are toothed in the Salmoninae and Thymallinae but are toothless in the Coregoninae.

MC. Meckel's cartilage, *cartilago meckeli*. Two slender rods of cartilage which extend forward from the endochondral portion of the angulars, along the mesial surface of the lower jaw to the dental symphysis.

MES. Mesopterygoid, *os mesopterygoideum* (endopterygoid, Goodrich, 1930; Harrington, 1955; entopterygoid, Berg, 1940; Gregory, 1951). A pair of thin, triangular intramembranous bones which comprise part of the palate and the floor of the orbit.

MSC. Mesocoracoid, *os mesocoracoideum*. A pair of curved endochondral bones which belong to the pectoral girdle and which act as braces between the cleithra, above, and the coracoids and scapulae, below.

MET. Metapterygoid, *os metapterygoideum*. A pair of semi-circular endochondral bones which fit into a curved area formed by the quadrate, symplectic, and hyomandibular bones.

N. Nasal, *os nasale*. A pair of small, tubular dermal bones which lie on the sides of the anterior tip of the frontals.

NA. Neural arch. The part of a vertebra which extends dorsally from the centrum and surrounds the spinal cord.

NS. Neural spine. The spines which are formed by the fusion of the paired neural arches and project dorsoposteriorly from the vertebral column.

OP. Opercle, *os operculum*. A pair of large, flat intramembranous bones which cover the gills.

OPO. Opisthotic, *os opisthoticum* (intercalary, Berg, 1940). A pair of small, conical intramembranous bones which cover the junction of the pterotic, epiotic and supraoccipital bones.

OS. Orbitosphenoid, *os orbitosphenoideum*. A median endochondral ossification which lies between the orbits and thus forms the floor and walls of the anterior end of the cranial cavity.

P. Parasphenoid, *os parasphenoideum*. A long, narrow, median intramembranous bone which forms the floor of the chondrocranium and extends from the vomer in front to the basioccipital, in the rear.

PA. Parietal, *os parietale*. A pair of dorsal roofing bones which lie posteriorly of and are overlapped by the frontals.

PAL. Palatine, *os palatinum* (autopalatine dermopalatine, Allis, 1897). A pair of splint-shaped mixed bones which lie along the margin of the palate, between the ectopterygoid and the premaxilla.

PAP. Parapophysis, *os parapophysis* (transverse process, Stokely, 1952). Paired, ventral, transverse processes which form articular surfaces for the ribs.

PB. Pharyngobranchial, *os pharyngobranchialium*. A pair of bones present in each of the first three gill arches. They form the most dorsal segment of the arch but only the first is attached to the parasphenoid. All three are attached to the epibranchials. Pharyngobranchials of the fourth pair are cartilaginous.

PCL. Postcleithrum, *os postcleithrum*. Three pairs of small, scale-like dermal bones which lie in a vertical series posteriorly of the cleithra and are present in all salmonid fishes.

PEFR. Pectoral fin ray (lepidotrichia, Goodrich, 1930). All rays of the pectoral fin, both rudimentary and principal.

PF. Prefrontal, *os praefrontale* (preorbital, Allis, 1898; lateral ethmoid, Berg, 1940). A pair of bones in the ethmoid region which are of dual origin (dermal and cartilage), and separate the olfactory capsule from the orbit.

PFR. Pelvic fin ray (lepidotrichia, Goodrich, 1930). All rays of the pelvic fin, both rudimentary and principal.

PM. Premaxilla, *os praemaxillare*. A pair of curved bones which form the anterior margin of the upper jaw. They are toothed in all species of salmonid fishes, at least during some period of their life history.

PO. Postorbital, *os postorbitalium* (circumorbitals, Ridewood, 1904a, 1904b). There are usually three pairs of thin, flat dermal bones which form the posterior rim of the orbit.

POP. Preopercle, *os praeoperculum*. A pair of curved dermal bones which lie just behind the suspensorium of the lower jaw and which partially cover the opercular bones.

POZ. Postzygapophysis, *os postzygapophysis*. Posterior projections which are borne on the neural arches and transverse processes and which function as articulating surfaces for the vertebrae.

PP. Pharyngeal plate, *os pharyngealium plattum*. Three pairs of small, toothed dermal plates which are found in the gill region. The first pair is borne on the third pharyngobranchials, the second pair on the fourth epibranchials, and the third pair on the fifth ceratobranchials.

PQ. Palatoquadrate, *cartilago palatoquadrata*. A pair of narrow cartilaginous strips which separate the quadrates from the mesopterygoid and metapterygoid bones. They are considered to be a remnant of the primitive upper jaw.

PRO. Prootic, *os prooticum*. A pair of large endochondral bones formed in the floor of the cranial cavity posterior of the orbit.

PRZ. Prezygapophysis, *os prezygapophysis*. Anterior projections which are borne on the neural arches and transverse processes and which function as articulating surfaces for the vertebrae.

PS. Pterosphenoid, *os pterosphenoideum* (alisphenoid, Gregory, 1933; Berg, 1940; Chapman, 1941a, 1941b; pleurosphenoid, de Beer, 1937). A pair of endochondral bones which lie dorsally of the prootics and posteriorly of the orbit.

PT. Posttemporal, *os posttemporale*. A pair of forked dermal bones which connect the pectoral girdle to the epiotic and opisthotic bones of the cranium.

PTG. Pterygiophore, *os pterygiopherium* (radials, Goodrich, 1930; Berg, 1940). A series of 3 endoskeletal rods which support the dorsal and anal fins. The pterygiophores are composed of 3 segments, a small, rounded distal bone, a short, horizontal middle bone and a long, pointed proximal bone.

PTO. Pterotic, *os pteroticum* (squamosal, Ridewood, 1904a; pterotic-intertemporal, de Beer, 1937; autopterotic, Harrington, 1955). A pair of mixed (cartilage and dermal) bones which lie on the posterolateral surface of the cranium. They bear the lateral temporal canals.

Q. Quadrate, *os quadratum*. A pair of triangular endochondral bones which articulate with the angulars of the lower jaw and thus connect the latter with the cranium.

R. Ribs, *costae*. The paired bones which surround the abdominal cavity and which are attached to the parapophyses or transverse processes. These are the pleural ribs.

RA. Retroarticular, *os retroarticulare* (angular, Ridewood, 1904a, 1904b; Gregory, 1933; Berg, 1940). A pair of small, triangular endochondral bones which are fused to the posterior corner of the angulars.

S. Scapula, *os scapulum*. A pair of flat endochondral bones located in the pectoral girdles which articulate anteriorly with the coracoids and posteriorly with the cleithra.

SC. Sclerotic cartilage, *cartilago sclerotica*. A pair of hemispherical cartilages which surround the eye balls. A small semilunar portion is partially ossified.

SCL. Supracleithrum, *os supracleithrum*. A pair of curved dermal bones located in the pectoral girdle which connect the cleithra with the posttemporals.

SE. Supraethmoid, *os supraethmoideum* (dermethmoid, Gregory, 1933; mesethmoid, Goodrich, 1930; Berg, 1940; Chapman, 1941a, 1940b; proethmoid, Dineen and Stokely, 1954; ethmoid. Harrington, 1955). The median dermal ossification that covers the hypethmoid (when present) and the underlying ethmoid cartilage.

SM. Supramaxilla, *os supramaxillare* (surmaxilla, Ridewood, 1904a; jugal, de Beer, 1937; Vladykov, 1954). A pair of thin, splint-like dermal bones which lie along the dorsal margin of the maxillae.

SO. Supraorbital, *os supraorbitalium* (circumorbitals, Ridewood, 1904a, 1904b; praeorbital, Vladykov, 1954). Two pairs of small curved bones which form the anterodorsal rim of the orbits. They do not bear sensory canals.

SOC. Supraoccipital, *os supraoccipitale*. A median bone which covers the posterodorsal surface of the cranium. A prominent crest of bone which extends backward from the endochondral portion is of dermal origin.

SOP. Subopercle, *os suboperculum*. A pair of thin, flat intramembranous bones which lie below the opercles and overlap the branchiostegal rays.

SP. Suprapreopercle, *os suprapreoperculum* (supratemporal, Parker, 1873; subtemporal, Gregory, 1933; de Beer, 1937; supraopercle, Holmgren and Stensiö, 1936). A pair of small, tubular intramembranous bones which are present in the salmonines. They lie above the preopercles and transmit the preopercular canal to the pterotic.

SPO. Sphenotic, *os sphenoticum* (autosphenotic, Holmgren and Stensiö, 1936; Harrington, 1955). A pair of conical endochondral bones which project anterodorsally from the otic region of the chondrocranium. In salmonids the sphenotic is separate from the dermosphenotic.

SY. Symplectic, *os symplecticum*. A pair of small, pointed endochondral bones which form part of the jaw suspension in bony fishes. They act as braces between the quadrates and the hyomandibulars.

U. Urohyal, *os urohyale*. A median intramembranous bone which lies in the muscles below the tongue.

UN. Uroneural, *os uroneurale*. Three pairs of bony plates which lie over the last 3 upturned vertebrae and the urostyle. They are believed to be remnants of neural arches. The larger, more anterior pair is sometimes called the caudal bony plate (Vladykov, 1954).

US. Urostyle, *cartilago urostyla*. In the restricted sense, this includes only the cartilaginous termination of the vertebral column which in salmonid fishes curves dorsad behind the last 3 upturned vertebrae.

V. Vomer, *os vomere*. A median dermal bone that is usually toothed and which lies at the anterior extremity of the roof of the mouth.

VE. Vertebra, *vertebra*. A series of bones which run the length of the body behind the cranium and comprise the vertebral column.

OSTEOLOGY OF THE GRAYLING, *THYMALLUS ARCTICUS*

The Olfactory Region

The olfactory or ethmoid region of the chondrocranium is pyramidal in shape with its anterior or rostral end short and bluntly rounded. Laterally the rostrum bears a cartilaginous knob which articulates with the maxilla anteriorly and with the palatine posteriorly. The slight expansion in this region also forms the anterior boundary of the olfactory capsule. The rounded anterior tip is capped by the paired premaxillae and roofed by the supraethmoid. Posteriorly the cartilage flares into two wing-like ossified projections, the prefrontals (or lateral ethmoids), which constitute the only ossification in the ethmoid complex in the grayling (Plate 1). The prefrontal is mainly endochondral, although there is a lamina of dermal bone on the outer surface. The anterior face of the prefrontal forms the rear margin of the olfactory capsule and its posterior face forms part of the anterior surface of the orbit. Below the prefrontal, a slight cartilaginous prominence provides a posterior articulation for the palatine. This second ethmopalatine articulation has been described by Swinnerton (1902) in *Gasterosteus aculeatus* and by de Beer (1927) in *Salmo trutta* (= *fario*). The cartilage mesial to the prefrontal is perforated by a foramen through which the olfactory nerve and the orbitonasal artery reach the olfactory capsule from the orbit. This is the *foramen olfactorium advehens* of de Beer (1927, 1937) and Böker (1913).

There are two other perforations in the ethmoid cartilage lying mesad of and somewhat above and below the olfactory foramen. These mark the exit of the superior and inferior oblique eye muscles. They meet the pair from the opposite side in the midline, where a deep anterior myodome has been formed in the ethmoid cartilage.

The Orbital Region

In the grayling little remains of the orbital region of the chondrocranium, it having been preempted by the large eye. The orbitosphenoid is completely lacking, leaving the paired pterosphenoids and the median basisphenoid as the only remaining ossification (Pl. 2, A and C). The use of the term pterosphenoid follows Goodrich (1930: 284), indicating that this bone in teleosts is not homologous with the pleurosphenoid of reptiles or the alisphenoid of mammals. Dorsally a flattened bridge of cartilage, covered by the frontals, connects the ethmoid region with the pterosphenoids. Even less remains of the ventral interorbital septum connecting the prefrontals with the basisphenoid. A median membranous septum separates the orbits. The pterosphenoids are rounded endochondral bones on the posterodorsal face of the orbits. Dorsally they border the large dorsal fontanelles. Posteriorly the pterosphenoids are united by cartilaginous sutures to the sphenotic and prootic bones. Ventrally and mesially the pterosphenoids protect the anterior part of the brain (Pl. 2, A and C). A small foramen for the trochlear nerve lies near the centre of each pterosphenoid.

The median Y-shaped basisphenoid lies just below the ventral part of the pterosphenoid (Pl. 2, A and C). Its short oblique arms articulate with the anterior edge of the prootics slightly anterior of the pituitary body and form the floor of the cranial cavity. The median ventral leg is separated from the parasphenoid by a small extension of cartilage, thus bisecting the posterior myodome. In *Salmo trutta*, according to de Beer (1937: 130), the basisphenoid is phylogenetically a cartilage bone which develops ontogenetically solely in membrane.

The eyeballs are surrounded by hemispherical sclerotic cartilages which have small semilunar ossifications at their anterior and posterior external surfaces. Each of these ossifications constitutes about one-sixth of the corneal perimeter.

The Otic Region

The Otic region is the best ossified part of the chondrocranium. Nearly all bones meet in jagged sutures, interspaced with cartilage, and with little overlap. All except the opisthotics and parts of the pterotics and supraoccipital, are endochondral bones. The most anterior are the subconical sphenotics which border the cartilage around the fontanelles dorsally and the orbit laterally (Pl. 1). They are covered by the frontals and dermosphenotics. The sphenotic is bordered anteromesially by the pterosphenoid, ventrally by the prootic, and posteriorly by the pterotic. Ventrally the sphenotic bears a lateral

fossa for the anterior articulation of the hyomandibular. Its inner surface is hollowed out to receive part of the anterior semicircular canal.

PTEROTIC. The pterotic is of dual origin, dermal and cartilaginous, the components being inseparably fused in the grayling (Pl. 1, A and 2, A). Its outer portion, bearing the lateral temporal canal, is described with the roofing bones. The deeper endochondral part of the pterotic fans out dorsally and ventrally, covering part of the otic capsule. The pterotic meets the sphenotic, dorsally, and the prootic and exoccipital, ventrally. There is a ventrolateral fossa for the posterior articulation of the hyomandibular. Dorsally the dermal part articulates with the frontal and occasionally with the parietal around the rim of the lateral temporal fossa. Its endochondral portion is separated from the dorsal fontanelle and supraoccipital by an expanse of cartilage. Posteriorly the pterotic meets the epiotic and exoccipital bones. This tripartite junction is capped by the small conical opisthotic. The inner surface of the pterotic is irregular and bears a deep cavern for the lateral semicircular canal (Pl. 2, C).

EPIOTIC. The epiotic is a pyramidal-shaped bone forming part of the dorsal and rear surface of the chondrocranium (Pl. 1, A and 2, B). The rounded upper surface of the epiotic lies between the pterotic and the supraoccipital, and forms the intermediate pair of five projections on the rear margin of the chrondrocranium. The other projections are lateral wings of the pterotics and the median supraoccipital crest. The posteriorly projecting point of the epiotic serves for the attachment of a strong ligament from the inner surface of the more dorsally directed prong of the posttemporal. Ventrally the epiotic curves inward to meet the exoccipital.

OPISTHOTIC. The opisthotic appears like a small cap over the cartilaginous junction of the pterotic, epiotic, and supraoccipital (Pl. 2, B). It is an intermembranous ossification in the strong ligament from the inwardly directed spine-like projection of the posttemporal, and is the only wholly non-endochondral bone of the otic region. It is so loosely attached to the chondrocranium and is so much a part of the ligament that it often comes off with the posttemporal when the latter is removed.

SUPRAOCCIPITAL. The supraoccipital is a median composite bone covering the caudodorsal surface of the cranial cavity. It is rounded, rising to a crest at the midline (Pl. 1, A and 2, A and B). Here a knob of bone protrudes between the parietals. This knob and the supraoccipital spine are of dermal origin. The supraoccipital extends forward beneath the parietals and forms the posterior margin of the dorsal fontanelles (Pl. 1, A). The dorsal fontanelles are separated by a narrow strip of cartilage (*taenia tecti medialis* of de Beer, 1937) (Pl. 1, A) derived from a posterior extension of the *tectum cranii* similar to that illustrated by Sanderson (1935) in the early development of *Salmo salar*. Less than a third of this median cartilage is ossified by the anterior growth of the supraoccipital, which occasionally extends forward to lie beneath the posterior margin of the frontals. Laterally the supraoccipital is in contact with the epiotics on either

side, but it is denied contact with the exoccipitals or the foramen magnum by a rather large expanse of cartilage. The spine extends caudally and forms a surface of attachment for fascia from the great lateral and protractor dorsalis muscles.

PROOTIC. Ventrally the brain is surrounded by the prootic, which forms the anterior floor of the cranial cavity (Pl. 1, B). It is the largest bone of the chondrocranium and consists of three diverging bony wings. A large expanse of bone extends dorsally to form the anterolateral wall of the brain cavity, another flange extends ventrally partly to enclose the posterior myodome, and a third extends to the midline to form the roof of the posterior myodome. Anteriorly and dorsally the prootic borders the pterosphenoid, sphenotic and pterotic. Posteriorly it is in contact with the exoccipital and basioccipital. Anteriorly and ventrally the prootic meets its mate from the opposite side and the lateral projection of the basisphenoid. The ventrally directed flange of the prootic is overlapped in part by a dorsal outgrowth from the parasphenoid. These two bones, plus the basioccipital, thus form the roof, sides and floor of the posterior myodome. Mesially parts of the anterior and lateral semicircular canals rest on the prootic and form the roof of the sacculus (Pl. 2, C). A vertical strut of bone partially divides the prootic into a portion facing anteriorly and another facing laterally. Three foramina pierce the lateral portion: a blood vessel (the head vein from the orbital sinus, according to de Beer, 1937, for *Salmo trutta*, the jugular canal of Holmgren and Stensiö, 1936) passes through the most ventral and mesial opening, next above is the large, posterior trigeminofacial foramen, and anteriorly is the palatine foramen for the palatine branch of the seventh cranial nerve. In the anterior-facing portion of the prootic the largest and most lateral foramen is the anterior trigeminofacial foramen, the smaller palatine foramen lies dorsal to it, and mesially is found the foramen for the abducens nerve.

BASIOCCIPITAL. The basioccipital forms the posterior floor of the cranial cavity (Pl. 1, B). It is a wing-shaped bone, its anterior flanges are overlapped by the parasphenoid ventrally and are in contact with the prootics anteriorly and with the exoccipitals dorsally. Posteriorly, the basioccipital is circular and articulates with the centrum of the first vertebra (Pl. 2, B). Mesially, it forms the lower halves of the large paired chambers that enclose the sacculus and the sagitta.

EXOCCIPITAL. The large exoccipitals are strongly convoluted and form the greater part of the rear of the cranium (Pl. 2, B). They are prevented from completely surrounding the foramen magnum by a narrow strip of cartilage dorsally and do not quite meet across the basioccipital. Ventrally they almost meet in a pair of rounded articular surfaces, the occipital condyles, which articulate with the atlas. The dorsal wing of the exoccipital meets the epiotic and the pterotic, and is slightly overlapped by the small opisthotic. The anterior wing of the exoccipital meets the prootic in front and borders the basioccipital throughout its ventral edge. The sidewalls of the exoccipital are pierced by the

small glossopharyngeal foramen, anteriorly, and by the larger jugular foramen for the vagus nerve, posteriorly.

OTOLITHS. Three otoliths lie within the auditory capsule. By far the largest is the sagitta, lying within the sacculus (Pl. 16, J3). It has a pointed rostrum anteriorly, and a mesal groove, the sulcus, dividing the otolith into dorsal and ventral portions (Frost, 1925). The asteriscus consists of a microscopic granule lying in the lagena (Pl. 16, J2). The lapillus is slightly larger, but still much smaller than the sagitta; it lies in the utriculus (Pl. 16, J1).

Investing Bones

DORSAL ROOFING BONES

SUPRAETHMOID. The supraethmoid is a small wing-shaped bone lying on the median dorsal surface of the chondrocranium, between the premaxilla and the frontals (Pl. 9, A). It arises as a small median ossification far forward between the premaxillae and grows both laterally and posteriorly. Anteriorly the supraethmoid is expanded to make contact with the ascending processes of the premaxillae, and posteriorly it is deeply bifurcate (Pl. 4), the two prongs thus formed having a number of slender projections which are overlapped by similar serrations from the frontals.

NASAL. The paired nasals are merely bony tubes enclosing the anterior parts of the supraorbital canals (Pl. 4). The cephalic canals of the lateral line system appear to influence the early deposition of bone cells, in that in those bones which bear canals the first ossification appears around the canals and then gradually spreads from these centres. This is true of the frontal, orbitals, extrascapulars and preopercle as well as the nasal. Thus, the nasal is already distinguishable in fish 35 mm in total length. It does not form a sutural connection with any bone but lies in the skin beside the supraethmoid-frontal suture.

FRONTAL. The frontals are large, triangular bones that cover most of the dorsal surface of the chondrocranium, including the dorsal fontanelles, and overhang the orbit laterally (Pl. 9, A). The frontal first makes its appearance in fish of 30 to 40 mm in length as an ossification around the supraorbital canal. Ossification continues in all directions with the greatest expanse of bone located medially and posteriorly from the original centre. The jagged anterior end of the frontal meets the supraethmoid, nasal, prefrontal, and first supraorbital, in that order, from the midline to the side. Laterally, behind supraorbital 1 the frontal forms about 20% of the perimeter of the orbit. At the rear of the orbit, the frontal articulates with the dermosphenotic. Caudolaterally a posterior projection of the frontal meets the dermal crest of the pterotic. The rear margin of the frontal sometimes comes in contact with the lateral temporal fossa, or it may be excluded by extensions of the pterotic and parietal. When in contact with the lateral temporal fossa, the frontal provides for part of the attachment of the lateralis profundus muscle (Greene and Greene, 1913). The remainder of the posterior margin of the frontal forms a broad transverse area of contact

with the parietal and overlaps it slightly. Dorsally, the pair of frontals forms a long and rather irregular suture at the midline, but diverge anteriorly where they are separated by cartilage. From the posterior end of the nasal bone the ossified supraorbital canal extends backward near the middle of the frontal, to a point above the posterior margin of the orbit, where it bends laterally and unites with the infraorbital canal on the dermosphenotic (Pl. 4).

PARIETAL. The paired parietals are irregular in shape and overlie much of the supraoccipital and a small posterior part of the dorsal fontanelles (Pl. 9, A). Each parietal begins as a small dermal centre of ossification some distance laterally of the midline. Each bone is slightly overlapped anteriorly by a backward growth of the frontal, and laterally it forms most of the dorsal border of the lateral temporal fossa. Posteriorly the parietals cover not only the supraoccipital but also part of the epoitics, and are themselves hidden by the extrascapulars. The parietals meet at the midline, except posteriorly, where they are separated by a small projection of the supraoccipital (Pl. 4).

EXTRASCAPULAR. The extrascapular bones consist of 2 or 3 bones on each side and a single median one in a transverse series over the posterior region of the skull between the parietals and the posttemporals (Pl. 9, A). They arise as separate centres of ossification surrounding the supratemporal canal. All are moderately expanded throughout (Pl. 4). The most lateral extrascapular is in contact with the ventral expansion of the posttemporal. The others continue in a half circle over the roof of the skull, to the posttemporal of the opposite side. They overlie and partly hide the pterotics, epiotics, supraoccipital, and parietals. Passing backward through the pterotic, the lateral canal enters the lateral extrascapular, where it is joined by the supratemporal canal, and transmits the combined branch backward to the posttemporal bone.

Only the posteriorly directed crest of the supraoccipital is seen from dorsal aspect (Pl. 9, A). The remaining endochondral portion is part of the otic capsule. The supraoccipital crest projects beyond the median extrascapular and between the dorsally directed prongs of the posttemporals. The crest forms a broad area of attachment for the protractor dorsalis muscle of the trunk (Greene and Greene, 1913).

The paired posttemporal and the pterotic bones are seen in part from dorsal view. The posttemporals are discussed with the pectoral girdle. The ectosteal portion of the pterotic (supratemporal-intertemporal, Holmgren and Stensiö, 1936; intertemporal, de Beer, 1937; membranopterotic, Harrington, 1955) originates as a small tubular bone enclosing the lateral temporal canal. Shortly after ossification commences the dermal part becomes fused with the underlying cartilaginous component. Anteriorly the pterotic articulates with the frontal and the dermosphenotic and receives the lateral canal from the dermosphenotic. Dorsally the pterotic forms the ventral margin of the lateral temporal fossa, and posteriorly it comes very near but usually does not touch the lateral extrascapular or the opercle. Ventrally and mesally the dermal portion of the pterotic curves inward and fuses with its cartilaginous component just dorsal of the articula-

tion with the hyomandibular. About midway in the pterotic, the lateral temporal canal is joined by the preopercular canal. Between the preopercle and the pterotic, the preopercular canal is membranous in the grayling; the tubular bone or suprapreopercle of the Salmoninae is absent (P. 10, B and C).

Lateral Skull Bones

Viewed from lateral aspect the head of *Thymallus arcticus* is almost completely invested in bone, except for the large orbit, the part of the adductor mandibularis muscle seen below the postorbitals, and the small part of the opercular muscles just above the dorsal tip of the preopercle.

Premaxilla. The premaxillae are a pair of slightly curved, somewhat triangular bones which comprise the anterior end of the upper jaw and the border of the anterior third of the gape (Pl. 10, B). They meet in a loose median suture in the adult. Each bone bears an anterior flange, to which a single series of 8 to 12 sharp conical teeth are attached, and a posterodorsal process which articulates with the anterolateral margin of the supraethmoid (Pl. 4). The remainder of the bone forms the anterior margin of the olfactory capsule. The lateral portion of the premaxilla overlaps the narrow mesal prong of the maxilla to which it attaches by a ligament and by which it is separated from the palatine The mesal portion of the premaxilla curves around the anterior extremity of the rostral cartilage, which separates it from the vomer ventrally. Each premaxilla arises as a small intramembranous ossification at the anterior tip of the ethmoid cartilage, and the teeth arise separately but grow toward the bone and fuse with it.

Maxilla. The maxilla, a thin bone comprising about two-thirds of the upper border of the gape, arises as a thin, splint-like ossification. The curved anterior end of the maxilla slips behind the premaxilla, where on one side it articulates with the premaxilla and on the other it articulates with the palatine. These are its only points of articulation. It is attached by skin and ligaments, dorsally and laterally, to the lachrymal, suborbitals, bones of the palate, and bones of the lower jaw. It bears a single file of 15 to 22 teeth except at the anterior and posterior ends of the bones, which are toothless (Pl. 4). The teeth arise separately, grow toward the maxilla, and fuse with it.

Supramaxilla. The single pair of supramaxillae lie on and partly cover the dorsal margin of the posterior half of the maxillae (Pl. 10, B). The supramaxilla is thin, narrow, and tapered at both ends, and like the maxilla it has cutaneous attachments to the suborbitals and bones of the palate (Pl. 4). It makes a belated appearance, long after the maxilla and teeth are fairly well ossified.

Circumorbital series. Ridewood (1904a; 69) has pointed out that because of the variation exhibited by the circumorbital bones no great morphological importance can be expected from a comparative study of them. This is true of the postorbitals of *Thymallus arcticus*, although the supraorbitals and the lachrymal remain constant in number and general shape. The circumorbital

series consists of 8 (occasionally 7) bones surrounding the greater part of the orbit, except for the part bordered by the frontal (Pl. 10, B). Authors have applied different names to the bones of the orbital series, for example Ridewood (1904b), Berg (1940) and Vladykov (1954). In the present treatise, the two anterodorsal bones are the supraorbitals, the anteroventral element is the lachrymal, the ventral bone is the infraorbital, the remaining posterior bones are postorbitals, of which the uppermost is the dermosphenotic. The supraorbitals are the only bones of the series which do not bear a sensory canal, and the area in which these bones develop is the last to ossify.

Supraorbital number 1 is small and somewhat arched dorsally (Pl. 4). Continuing from the rim of the frontal, it forms the anterodorsal margin of the orbit. Anteriorly it lies over the prefrontal, which it may touch without articulation. Its anteriormost tip forms a narrow contact with supraorbital 2.

Supraorbital number 2 is unlike the other circumorbital bones (Pl. 4). It is narrow and U-shaped, forming part of the anterior margin of the orbit and the posterior margin of the nasal capsule. One of its arms curves inward to overlap the prefrontal. Ventrally it forms a broad suture with the lachrymal.

The lachrymal is roughly rectangular in shape with a small dorsally directed projection (Pl. 4). It forms part of the anterior rim of the orbit and lies just above the maxilla. It carries the anterior extension of the infraorbital canal, where that canal branches into 3 to 5 short canals that terminate in external pores. The lachrymal articulates anteriorly with supraorbital number 2, and posteriorly with the infraorbital.

The infraorbital bone is thin and subtriangular, with the apex pointing forward (usually more attenuate than in the specimen figured, Pl. 4). The apex projects beneath the lachrymal for a short distance. It carries the infraorbital canal; it articulates with the lachrymal anteriorly, and with postorbital number 1 posteriorly.

Postorbitals 1, 2, and 3 are thin plates forming the posterior rim of the orbit. They are similar in shape, although postorbital 1 narrows anteriorly where it meets the infraorbital (Pl. 4). These bones almost completely cover the large adductor mandibularis muscle and touch the preopercle along part of their posterior margins (Pl. 10, B). These are the most variable of the circumorbitals, occasionally fusing to form two bones instead of 3. All carry the infraorbital canal. Dorsally postorbital 3 articulates with the dermosphenotic. This bone differs little from the other postorbitals but it is distinctive in being somewhat smaller and in bearing the junction of the supraorbital and infraorbital canals to form the lateral canal (Pl. 4), The dermosphenotic articulates dorsally, with the frontal, and ventrally with postorbital 3. It borders the orbit anteriorly, and the pterotic posteriorly (Pl. 10, B).

DENTARY. The dentaries are a pair of V-shaped bones forming the major supports of the lower jaw (Pl. 4). Their apices meet anteriorly in a loose symphysis and their two limbs curve sharply around the margin of the jaw. The upper limb is shorter, and its anterior three-fourths bears a single row of approxi-

mately 18 teeth. It connects posteriorly to the rear end of the maxilla by a fold of skin and draws that bone into a vertical position as the lower jaw is depressed, thus widening the gape. The lower limb is longer and encloses the mandibular canal. This limb extends caudad as far as the quadrate but does not touch the retroarticular (Pl. 4). The crotch of the dentary envelops the angular, and Meckel's cartilage is almost completely embedded in nearly the entire length of its mesal surface (Pl. 5). The anterior part of the dentary is endochondral, and is termed the mentomeckelian bone (de Beer, 1937; Harrington, 1955). It is continuous with the intramembranous part of the dentary, which commences early as two ridges corresponding to the two limbs.

ANGULAR. The angular is the second largest bone in the lower jaw (Pl. 4); only the dentary is larger. The angular is a controversial bone, because its origin and development are somewhat obscure (de Beer, 1927, 1937; Haines, 1937; Harrington, 1955). Most past writers have termed it the articular, but the findings of Haines (1937) and Lekander (1949), discussed by Berg (1940: 416) and Harrington (1955: 284), demonstrate the desirability of applying the name angular. The small bone at the ventrocaudal end of the mandible, commonly termed angular in the past, may be called the retroarticular (Harrington, 1955: 287). The bone here termed the angular arises, in part, as an endochondral ossification at the posterior end of Meckel's cartilage, but most of it arises intramembranously. The angular is thin and toothless. It forms an acute angle anteriorly where it slips into the dentary, and it is arched in cross section throughout most of its length, the grooves on its mesal surface being occupied by Meckel's cartilage. Lying well back on the cartilage is the coronomeckelian (Pl. 5). The angular is massive posteriorly; on its upper surface there is a deep transverse depression, which articulates with a ventral bar on the quadrate. The mandibular canal passing from the preopercle to the dentary penetrates the outer face of the angular with a short, oblique tube (Pl. 4). As usual, ossification appears early around this sensory canal. Like the dentary, the upper margin of the angular is connected to the maxilla by a fold of skin. A ligament attaches the posterior end of the angular to the preopercle.

RETROARTICULAR. The retroarticular is a small triangular bone located at the caudoventral corner of the mandible (Pl. 4 and 5). It is inseparably fused to the angular, and in the grayling does not come in contact with the articular facet. It is composed mainly of dermal bone although it does have a small core of endochondral material.

CORONOMECKELIAN. The coronomeckelian (Harrington, 1955: 285), usually called sesamoid articular, is a small triangular bone of dermal origin, located on the mesal surface of the angular bone and loosely attached to Meckel's cartilage (Pl. 5). It provides for a part of the insertion of the adductor mandibularis muscle, and according to Ridewood (1904a) is an ossified tendon.

PREOPERCLE. The preopercle, despite its name, does not belong to the opercular series (Ridewood, 1904a; Hubbs, 1919). The preopercle carries the

sensory canal of the same name and is therefore likened to the circumorbitals by some workers (Ridewood, 1904a; Westoll, 1937). Functionally the preopercle serves in several ways: its anterior margin offers a broad area for the origin of the large adductor mandibularis muscle, its expanded posterior part helps shield the gills, and it carries the preopercular canal. It arises as a narrow arched ossification in close proximity to the canal, and expands posteriorly and ventrally with growth. It is sculptured with branches of the sensory canal, especially in its expanded ventral part, where occasionally 3, but usually 4 pores open to the exterior. The preopercle of the adult grayling is prominently arched; the horizontal arm is about two-thirds the length of the vertical arm (Pl. 4). The preopercle does not articulate with any other bone, but the anterior tip of its horizontal arm is attached to the jaw articulation by a strong ligament. Mesally the preopercle covers part of the ceratohyal, epihyal, quadrate, symplectic, hyomandibular, the three opercular bones, and all of the interhyal, to which it is attached by skin and ligaments. Anteriorly the postorbitals usually touch the preopercle along the length of the vertical arm (Pl. 10, B). Dorsally the preopercular canal is transmitted directly to the pterotic, as the grayling does not have a suprapreopercular bone.

OPERCULAR SERIES. The larger elements of the operculum are believed to be expanded branchiostegal rays, homologous with the saber-like rays. All elements of the opercular series are entirely dermal in origin. The opercle is the largest bone in the grayling skull. It is thin, smooth and rectangular and covers much of the gill arches (Pl. 4). It first appears as a small dermal ossification around the articulation with the hyomandibular, and spreads backward and downward from this point. The anterior border of the opercle is overlapped by the preopercle (Pl. 10, B) and ventrally it narrowly overlaps the subopercle. The latter denies the opercle contact with the interopercle. Dorsally it is free, but here it partially covers the dilator operculi, levator operculi, and adductor operculi muscles, all of which insert on the mesal surface of its dorsal half (Greene and Greene, 1913). When the opercle is closed, the posterior border of the opercle extends over the anterior part of the supracleithrum. The inner surface of its anterodorsal corner is thickened and has an oval depression for articulation with the hyomandibular.

The subopercle, when it first ossifies, looks very much like a thin, flat, branchiostegal ray, but later it expands posteriorly into a flat plate (Pl. 4). Its ventral border overlaps the last (9th or 10th) branchiostegal ray; anteriorly, it is partly covered by the interopercle, and its small pointed, proximal projection is hidden by the preopercle (Pl. 10, B). When the operculum is closed, the dorsal edge of the subopercle covers the anterior part of the cleithrum, supracleithrum, and first postcleithrum.

The interopercle is a thin triangular bone covering the lower part of the gill region (Pl. 4). It originates as a small triangular ossification much like the branchiostegal rays, except that it is out of position and does not form a series with them. For this reason, some workers (e.g. Ridewood, 1904a) consider it to belong with the preopercle rather than in the branchiostegal series. Hubbs

(1919), however, included it with the latter group. Ventrally the interopercle partly covers the last branchiostegal ray and the epihyal bone; posteriorly it overlaps the subopercle (Pl. 10, B); while anteriorly and dorsally nearly half the bone is hidden by the preopercle.

The branchiostegal rays first appear as thin bony strips on the ventrolateral side of the head. The usual number is 9 or 10, and there may be 9 on one side and 10 on the other. The first anteroventral ray is the smallest, and those above are progressively longer and more expanded (Pl. 10, B). The first 6 or 7 rays are attached to the ceratohyal and the upper 3 to the epihyal bone. They are arranged in a series with each ray partly overlapping the one in front of it.

Ventral Bones of Cranium

Vomer. The vomer, is a small, oval, median bone in the anterior part of the roof of the mouth (Pl. 4). Ventrally it carries 7 or 8 weak teeth which are borne on two ridges which project from the rest of the bone. Dorsally the vomer is convex upward in transverse and longitudinal sections (boat-shaped), the dome fitting into a depression in the cartilaginous rostrum. Anteriorly the vomer is curved to conform to the border of the rostrum and posteriorly it consists of two acute prongs which overlap the parasphenoid. The vomer arises intramembranously as a small rounded ossification.

Parasphenoid. The parasphenoid is a long, narrow intramembranous bone covering most of the ventral surface of the chondrocranium (Pl. 4). It bears a marked dorsal ridge, which fits into a groove in the cartilaginous ethmoid and interorbital septum, from near the anterior tip to as far back as the basisphenoid. In the midline is a small, spine-like dorsal projection that points towards the basisphenoid and is joined to the ventral leg of that bone by cartilage. Behind this projection, the parasphenoid forms a deep trough, having lateral flanges of bone that curve dorsad to form the floor and part of the side walls of the posterior myodome. These flanges contact similar downward-projecting flanges from the sides of the basioccipital and both prootics. Anteriorly the flanges are somewhat elevated and serrate; behind this they are smooth and straight (Pl. 4). The V-shaped posterior end of the parasphenoid does not quite touch the atlas, but it does leave a posterior opening in the myodome. Anterolaterad of the median dorsal spine are a pair of foramina through which the internal carotid arteries pass. Posterolaterad of the same spine, the posterior palatine branch of the facial nerves pass through a second pair of foramina. In lateral aspect, the parasphenoid is bent abruptly downward at the level of the palatine foramina, the bone rising gradually both before and behind that point.

Visceral Arches

Introduction

The bones discussed in this section are homologous to the cartilaginous elements of the upper jaw, hyoid arch and the 5 branchial arches of the shark. The bones of the palatoquadrate no longer border the gape, but constitute an

"inner jaw", primarily concerned with jaw articulation and development of the palate. The remainder of the primitive mandibular segment (Meckel's cartilage) was discussed with the bones of the lower jaw, namely the dentary and the angular. The hyoid apparatus suspends the jaws from the cranium and, through the hypohyals, provides the anterior and inferior skeletal support of the gill arches. The first 4 branchial arches support the gills. The 5th arch is incomplete and does not function in respiration.

Palatoquadrate Arch

Palatine. The palatine is a splint-shaped bone of mixed origin. It arises as a thin strip of cartilage running forward from the quadrate and lying beneath the orbit (autopalatine of Allis, 1897: 772). Ventrad of the endochondral part there appears a separate dermal ossification, the dermopalatine (Allis, 1897: 772). Below the dermopalatine, the teeth appear as individual centres of ossification. The teeth fuse to the lower edge of the dermopalatine and the latter fuses with the autopalatine to form the mixed palatine bone. The anterior end of the palatine is larger and bears 8 to 12 small, somewhat retrorse teeth that form a single irregular row (Pl. 5). The palatine articulates mesally with the chondrocranium at two points, one in front and one behind the nasal capsule, in a manner described by Swinnerton (1902) for *Gasterosteus aculeatus*, by de Beer (1927) for *Salmo trutta*, and by Saunderson (1935) for *Salmo salar*. The anterior or rostro-palatine articulation (de Beer, 1937) bears a cartilaginous knob which fits into a depression formed partly by the incurved maxilla and partly by the enlargement of the rostrum. The posterior ethmopalatine articulation (de Beer, 1937) consists of a small cartilaginous projection which attaches to the ethmoid cartilage just beneath the prefrontal. The remainder of the lateral edge of the palatine is separated from the mesopterygoid by a strip of cartilage. The posterior end of the palatine is slightly overlapped by the ectopterygoid, thus separating the former from the quadrate. The lateral margin of the palatine has a ligamentous attachment to the maxilla.

Ectopterygoid. The ectopterygoid is a small, curved, dermal ossification forming the lateral margin of the palate (Pl. 5). Its dorsal border lies near the mesopterygoid but is narrowly separated from it by cartilage. Posteriorly the ectopterygoid lies against the anterior border of the quadrate, and anteriorly it is in contact with the palatine. The ventral margin of the ectopterygoid is free, being connected to the maxilla by a loose fold of skin.

Quadrate. The quadrate is a fan-shaped endochondral bone articulating with the depression in the angular (Pl. 5). The area on and around its articular condyle is the first to ossify during development. Dorsally the quadrate is separated from both the mesopterygoid and metapterygoid by a narrow strip of cartilage, the palatoquadrate cartilage, which continues forward and meets the palatine. Posteriorly the quadrate bears a thin, acuminate strut of dermal bone, the grooved lower side of which receives the upper edge of the horizontal limb of

the preopercle. Between this strut and the main part of the quadrate lies the symplectic, connecting the quadrate with the hyomandibular.

MESOPTERYGOID. The mesopterygoid lies just in front of the metapterygoid. It is a thin triangular bone whose dorsal edge is directed inward, with most of the expanded surface lying under the eyeball (Pl. 5). It covers much of the palate but does not quite touch the parasphenoid. The hind border is overlapped by the metapterygoid and is separated from the quadrate by a bridge of cartilage. The entire outer margin of the mesopterygoid is bordered by the ectopterygoid and the palatine, and the pointed anterior end touches the ethmoid cartilage beneath the prefrontal. It arises intramembranously, ossification beginning at its outer margin.

METAPTERYGOID. The metapterygoid is a semilunar endochondral bone fitting into the curve formed by the quadrate, symplectic, and hyomandibular. Anteriorly it bends slightly inward, forming a part of the ledge on which the eyeball rests (Pl. 5), and overlapping the posterior margin of the mesopterygoid. Dorsally it is free, forming part of the lateral wall of the pharynx. Posteriorly it overlaps the lower part of the hyomandibular, and ventrally it is connected to the symplectic and quadrate by a narrow strip of cartilage.

HYOID ARCH

HYOMANDIBULAR. The hyomandibular is a hatchet-shaped endochondral bone that suspends the jaws from the cranium (Pl. 5). It contains a hyomandibular foramen, through which a branch of the facial nerve passes. The foramen extends from the mesal surface of the upper part of the bone to the deep groove below the posteriorly directed opercular condyle. Anteriorly on the bone is a thin dermal flange that is overlapped by a posteriorly directed process from the metapterygoid. Dorsally the hyomandibular articulates with the sphenotic and pterotic, by an elongate condyle that retains a cartilaginous surface. Below the opercular condyle, the ventral projection of the hyomandibular is overlapped by the preopercle. Ventrally the hyomandibular is connected to the symplectic and the interhyal by a wedge of cartilage. The hyomandibular is overlain by the large adductor mandibularis muscle and by the postorbitals. Ossification first appears in a Y-shaped cartilaginous area around the hyomandibular foramen.

SYMPLECTIC. The symplectic, an endochondral bone peculiar to fishes, serves as a brace for the articulating bones of the jaw. It is shaped like a marlin spike, pointed anteriorly, where it is in contact with the quadrate (Pl. 5). It is united to the hyomandibular and metapterygoid by a narrow bridge of cartilage.

INTERHYAL. The interhyal is a small, cylindrical endochondral bone which connects the posterodorsal tip of the epihyal with the triangular piece of cartilage which separates the symplectic from the hyomandibular, and thus suspends the lower hyoid elements from the hyomandibular (Pl. 5).

EPIHYAL. The epihyal is a semilunar bone of endochondral origin. Its broad anterior end articulates with the ceratohyal, and the posterodorsal tip is connected to the interhyal (Pl. 5). Three branchiostegal rays are borne on the epihyal.

CERATOHYAL. The ceratohyal is a flat endochondral bone extending along the side of the pharyngeal cavity. Both ends are somewhat expanded, the wider posterior end articulates with the epihyal, and the narrower anterior edge joins the hypohyals (Pl. 5). Six or 7 branchiostegal rays are suspended from it.

HYPOHYAL. The hypohyals consist of two pairs of conical endochondral bones connecting the pair of ceratohyals with the median basihyal. Both the upper (smaller) and lower (larger) hypohyals meet their fellows from the opposite side at the midline, in a suture that is covered dorsally by the first two (median) basibranchials (Pl. 5). The upper and lower hypohyals are separated by cartilage where the anterior cartilaginous tip of the ceratohyal meets the hypohyals. Anteriorly the hypohyals join the basihyal cartilage.

BASIHYAL. The median basihyal forms the base of the tongue (Pl. 5 and 6, C). It is entirely cartilaginous, but it is covered dorsally by a thin, spatulate, dermal ossification, the lingual plate (Pl. 5 and 6, C), which bears a central patch of weak teeth. Posteriorly the basihyal articulates with the paired hypohyals, their junction lying beneath the first basibranchial. The hyoid elements of the grayling are similar to those of *Salmo salar* which have been described by Tchernavin (1938b).

BRANCHIAL ARCHES

The branchial skeleton of the grayling is largely endochondral in origin, and much of the cartilage is retained, especially at the articular surfaces and in the anterior and posterior copula (Tchernavin, 1938b). Only the dentigerous pharyngeal plates are intramembranous.

PHARYNGOBRANCHIALS. There are 3 pairs of Y-shaped pharyngobranchials, each with 3 articular surfaces (Pl. 6, C). Only the first bone in the series is attached to the ventral surface of the parasphenoid. Its remaining two articular surfaces are joined to the epibranchial of the first arch and to a knob of cartilage which connects with the pharyngobranchial of the second arch, respectively. The second pharyngobranchial has a broad lateral base that is in contact with its own epibranchial, and an anterior petiole-like branch that makes contact with the epibranchial of the first arch. A broad projection with an expanded mesal end connects with slender prongs from the 1st and 3rd pharyngobranchials. The third pharyngobranchial articulates broadly with its own epibranchial and by slender branches with the epibranchial and the pharyngobranchial of arch 2. The 3rd pharyngobranchial bears a small toothed plate on its lower surface (Pl. 6, C). A small piece of cartilage, regarded as the pharyngobranchial of the 4th arch, connects epibranchial 4 with the expanded lateral wing of pharyngobranchial 3. The pharyngobranchials are without gill rakers.

EPIBRANCHIALS. The first 4 pairs of branchial arches have epibranchials. The first three of these are similar, each bearing a well-developed posterior prong, mentioned above, and a deep groove on its upper surface which forms a protective cradle for the afferent and efferent branchial arteries. The 4th epibranchial has an expanded dorsal portion and a toothed pharyngeal plate lying partly on its ventral surface and partly on the cartilaginous 4th pharyngobranchial (Pl. 6, C). The plate is not fused to the branchial bones. The first 3 pairs of epibranchials bear short gill rakers both anteriorly and posteriorly, but those on the posterior edge are much smaller and fewer in number. The 4th epibranchial, however, bears no gill rakers.

CERATOBRANCHIALS. There are 5 pairs of ceratobranchials (Pl. 6, C). They are the longest bones in the branchial arches. Each one, except the last, has a groove on its ventral surface which partly surrounds the branchial arteries. All 5 ceratobranchials bear gill rakers on their anterior edges, but those on the posterior edges are shorter, and they are lacking altogether on the fifth. The 5th ceratobranchial is somewhat expanded near its base, and it bears a toothed pharyngeal plate on its dorsal surface (2 in one specimen). The first 3 ceratobranchials articulate anteromesially with their hypobranchials and the last two articulate with the posterior copula.

HYPOBRANCHIALS. Only the anterior 3 arches possess hypobranchials. The first two are similar and both articulate with the anterior copula at the cartilaginous bridges between the basibranchial bones. The 3rd hypobranchial is widest at its articulation with the ceratobranchial, becoming narrower as it arches around the 4th basibranchial (Pl. 6, C). All three bear short gill rakers on their anterior edges only.

BASIBRANCHIALS. The 4 basibranchial bones lie in a median series on the floor of the pharynx (P. 6, C). These, together with interspaced cartilage, constitute the anterior copula (Tchernavin, 1938b: 350). The posterior copula, composed of a broad plate and a tail piece lying between the 5th ceratobranchials, is entirely cartilaginous. The 3rd pair of hypobranchials connect the posterior copula with the 4th basibranchial of the anterior copula. The 1st basibranchial lies between the hypohyals; anteriorly it joins the basihyal cartilage and, posteriorly, it forms a suture with the 2nd basibranchial, without intervening cartilage. In the grayling, the basibranchials are not covered by a basibranchial plate.

UROHYAL

UROHYAL. The urohyal does not belong to the branchial skeleton but arises as an intramembranous bone (Ridewood, 1904a: 76); it is included here only for convenience. The small, rounded anterior knob of the urohyal is attached to the hypohyals by a ligament. Posteriorly, the urohyal broadens to form lateral flanges on its ventral surface. The thin crest extends dorsally like a sail, with a jagged posterior margin (Pl. 5). The urohyal is located dorsal of the branchio-

stegal rays, the intermandibularis, geniohyoideus, and hyohyoideus muscles. The urohyal is the ossified tendon of the sternohyoideus muscles, in which it is embedded. The muscles originate at the anterior ends of the cleithra and coracoids and run forward to insert on the hypohyals and the dorsal crest of the urohyal.

Axial Skeleton

Vertebral Column

The vertebral column is composed of 59 to 61 vertebrae (58 to 62 in *T. arcticus baicalensis* and 56 to 61 in *T. thymallus*, Svetovidov, 1936), counting all distinguishable centra but not the largely cartilaginous urostyle, in the manner of Vladykov (1954) and Andrews and Lear (1956). Of these, 36 to 39 are trunk vertebrae and 21 to 23 are caudal vertebrae with haemal spines.

The centra are hour-glass shaped and amphicoelous, and each is perforated by a small median canal. The hollowed out spaces between the centra, as well as the canals are filled with the remains of the notochord. The first vertebra, or atlas, articulates with the basioccipital and with the exoccipitals; it varies in size, but is usually shorter than the other centra. The second vertebra is somewhat larger, and the remaining ones increase in size to the middle of the trunk region, after which they gradually decrease in size. The lateral face of each centrum is marked by horizontal bony ridges which are areas of origin and insertion for fascia from the myotomes.

Dorsally the centra bear neural arches which are larger and heavier cranially, and become smaller and lower caudally (Pl. 7, A and B). The neural arches bear paired anteriorly and posteriorly directed projections, the dorsal pre- and postzygapophyses (Pl. 7, B). The prezygapophyses do not quite touch the postzygapophyses. The neural arches terminate in posteriorly directed neural spines (Pl. 7, A). Those lying before and below the dorsal fin consist of separate lateral elements, most of the remainder are fused above the neural cord to form acute conical spines, and the last 6 or 7 are blunt and flat (Pl. 7, C). The anterior neural arches are broad and occupy the entire length of each centrum, with the spines emerging above the middle of the vertebrae (Pl. 7, A). The first 24 to 26 neural arches are not co-ossified with the centra, a feature characteristic also of the Argentinidae and Clupeidae (Ford, 1937: 36). In the tail region, the neural arches are firmly fused to the centra, are tilted more strongly caudad and the spines emerge farther forward over the centra (Pl. 7, B).

Epineurals, small dorsolateral intermuscular bones, articulate with the bases of the neural arches along the first 25 to 28 vertebrae (Pl. 7, A). All are about the same length, but the more posterior ones articulate higher on the neural arches.

The vertebrae bear paired ventral transverse processes, parapophyses, which occupy most of the length of each centrum. The parapophysis of the atlas consists merely of a bony nodule and does not have a rib. That of the second vertebra is somewhat atypical and occasionally supports a short rib. Approximately the first 25 parapophyses, including the above two, lie in pits in the centra (Pl.

7, A). They are not fused to the centra but are held firmly in place by ligaments (Ford, 1937). The parapophyses bear ventral pre- and postzygapophyses which function as articulating surfaces for the vertebrae (Pl. 7, B). The ventral prezygapophyses in the anterior trunk region are somewhat better developed than the postzygapophyses; each has an anterior projection which extends forward toward the centrum next anterior but does not quite articulate with the postzygapophysis.

Behind these anterior 26 vertebrae, the transverse processes increase in length and are ankylosed to the centra. A transverse bony bridge connects the transverse processes in each of the 2 or 3 most posterior trunk vertebrae, thus forming a closed haemal arch on each vertebra. The remaining haemal arches of the more posterior vertebrae project ventrally, forming haemal spines (the distinguishing feature of the caudal vertebrae, Pl. 7, B). The haemal spines of the posterior 8 to 10 vertebrae are gradually expanded into the hypurals of the tail. The haemal canal contains the caudal artery and vein, and is open as far as and sometimes through the first hypural.

The ventral or pleural ribs curve ventrally between the muscles and peritoneum around the peritoneal cavity, ending in cartilaginous points near the midline. The ribs belonging to vertebrae 3 through 20 are best developed, being larger and longer, and somewhat expanded dorsoventrally. These also have a T-shaped head, with surfaces which articulate with the parapophyses (Pl. 7, A). The more posterior ribs have progressively blunter, flatter heads, which are attached by ligaments near the tips of somewhat lengthened transverse processes. These ribs also decrease in size, caudally, until the last is little more than a bony spur, similar in form to a haemal spine. There are from 35 to 38 pairs of ribs; the first and occasionally the last trunk vertebrae do not bear ribs. From the bases of ribs 3 through 10, short epipleural ribs project caudally (Pl. 7, A) as spine-like intermuscular processes.

The caudal fin of the grayling is a large forked structure consisting of 7 or 8 centra, modified neural and haemal structures, and fin rays. It is finely scaled far out on the rays, especially on the dorsal and ventral lobes. The last 7 or 8 vertebrae are somewhat modified to support the fin, regressing in size and carrying expanded neural and haemal spines which project backward. As in other salmonid fishes, the 3 terminal vertebrae are upturned and become progressively smaller. The antepenultimate vertebra is only slightly upturned and is usually intermediate in size and shape between the two adjacent vertebrae. The last vertebra with a discernible centrum is the most highly modified.

Of the modified neural spines (from the last 8 vertebrae) the anterior 3 or 4 are fused with the neural arch, the next 1 or 2 are free from the neural arch (Pl. 15, C), and the 2 epurals are free from the anterior (first) uroneural (Pl. 7, C). The first uroneural and the 3 neural arches before it are free from the centra. The anterior uroneural has 2 small dorsal depressions which act as articulating surfaces for the epurals. The caudal ends of the epurals are almost straight across, similar to the hypurals.

Three pairs of uroneurals are present, beside and partly covering the last

4 centra and the urostyle (Pl. 7, C). The uroneurals are readily distinguishable since they are paired structures, whereas the epurals are unpaired. Regan (1910) and Hollister (1936) interpreted the uroneurals as specialized neural arches. Both of these authors included among the uroneurals the caudal bony plate of Vladykov (1954) or extra neural arch of Dineen and Stokely (1954). Except for a difference in position, there is no apparent reason to doubt that these 3 pairs of bones are serially homologous. The anterior uroneural is a paired bone covering the dorso-lateral surface of the last 3 or 4 centra; it bears a posterior projection that extends well onto the urostyle (Pl. 7, C). The anterior uroneural is forked, the more lateral limb of the fork being slightly longer. The dorsal crest is small. The second uroneural, lying dorsolateral of the urostyle, is larger than the third and partly covers both the first uroneural and the urostyle. The ventrolateral surface of the small third uroneural overlies the urostyle (Pl. 7, C).

The vertebral column terminates in the cone-shaped urostyle. The urostyle is curved abruptly dorsad beyond the last centrum and terminates near the bases of the longest rudimentary caudal rays (Pl. 7, C). Although usually considered cartilaginous in the Salmonoidei, the urostyle is not completely so in the adult grayling. Two or 3 bony nodules are embedded in a cartilaginous matrix, the largest nodule being an ossified core just beyond the terminal centrum.

Developmentally, ossification commences earlier around the upturned notochord than it does farther forward. In this posterior area, the first uroneural shows signs of ossification simultaneously with the appearance of bony material in the neural arches just in front of it. The penultimate and ultimate centra begin to ossify before the 5 or 6 centra anterior to them. The first uroneural appears to be formed by a fusion of the posterior neural arches belonging to at least the last 3 vertebrae. The 2 epurals are probably modified neural spines which have not become fused to the first uroneural. It is interesting that the 1 or 2 neural spines just anterior of the epurals ossify separately from their neural arches and do not fuse with the latter even in the adult (Pl. 7, C).

Haemal spine modification begins with those belonging to the last 7 or 8 caudal vertebrae (Pl. 7, C). There is a broadening of both the haemal arch and spine, with the distal end becoming flat and expanded. The haemal spines lying ventral of the urostyle and the last 3 centra are the most highly modified and are termed hypurals. They support the principal caudal fin rays. In the grayling, there are 7 hypurals and 5 other modified haemal spines anterior of them (Pl. 7, C). Developmentally ossification commences in the haemal arches and spines a little before bony material is present in the centra. The first (and sometimes the 2nd) modified haemal arch (8th last vertebra) is most often fused to its centrum. The remainder, including the hypurals, are autogenous (Regan, 1910). The 7 hypurals are numbered, starting anteriorly with number 7 lying nearest the urostyle. Hypural 1 is associated with the 1st (antepenultimate) upturned caudal vertebra; hypurals 2 and 3 are associated with the 2nd (penultimate) upturned vertebra; hypurals 4 and 5, with the terminal (ultimate)

vertebra; and hypurals 6 and 7, with the urostyle (Pl. 7, C). Since the hypurals are modified haemal spines this distribution suggests that each of the last 2 vertebrae and the urostyle represents 2 fused centra, 6 in all.

The caudal fin rays are supported by the modified neural spines, epurals, urostyle, hypurals, and modified haemal spines. The long rays which extend the whole length of the fin are counted separately from the short rudimentary rays that are located dorsally (epaxial) and ventrally (hypaxial). All principal rays are branched, in the adult, except the outer dorsal and ventral rays. The frequencies of occurrence of the principal rays of 15 *T. arcticus* were as follows: 17 (1), 18 (3), 19 (11); whereas 11 specimens of *T. thymallus* yielded the following counts: 18 (4), 19 (7).

Median Fins

Thymallus arcticus is characterized by its long dorsal fin, with between 18 and 25 rays including the short, crowded forward rays. Counts made on 11 specimens of *T. thymallus* yielded the following distribution: 18 (1), 19 (6), 20 (4), whereas Svetovidov (1936: 215) reported 17 to 22 rays in *T. arcticus baicalensis*. The first 8 or 10 rays are unbranched but all are paired. Each ray is supported by a chain of 3 pterygiophores. These include a small rounded pterygiophore which is clasped between the base of each paired ray. The 2nd series of pterygiophores are somewhat larger, rod-like and function as spacer bars between the bases of the rays. The 3rd series are long, dorsally expanded pterygiophores which insert between the neural spines. The first of the elongate pterygiophores is slightly heavier than the others and supports 2 or 3 of the anterior fin rays. It is inserted between the neural spines of vertebrae 12 and 13, or 13 and 14. The long pterygiophores are expanded dorsally, forming a more rigid support for the rays. There usually are 2 or 3 fewer pterygiophores than dorsal rays. In front of the pterygiophores of the dorsal fin there are about 12 ossified interneurals supported between the bifurcated neural spines (Pl. 7, A). The first is the largest and heaviest.

An adipose fin which does not contain any ossified elements or bony support is present.

The anal fin has from 13 to 15 rays. The first 4 or 5 of these are unbranched. The skeleton of the anal fin is similar to that of the dorsal fin, each ray supported by 3 ossifications separated by cartilage. A small distal pterygiophore lies between the two arms of each ray, an intermediate horizontal pterygiophore lies embedded in muscle between that ray and the one next posterior, and a proximal long pterygiophore, directed anterodorsally is inserted between the haemal spines (Pl. 7, B). The distal ends of the proximal elements are not expanded as in the dorsal pterygiophores. There are fewer pterygiophores than rays, the usual number being 11 or 12. The last 2 and the first 2 fin rays are supported by single pterygiophores. The first proximal pterygiophore is most often inserted between the last trunk and first caudal vertebrae.

Appendicular Skeleton

Pectoral Girdle

The pectoral girdle consists of 9 paired bones which have a ligamentous attachment to the skull, dorsally, and which curve ventrally so that the cleithra lie beneath the pharynx.

Posttemporal. The pectoral girdle is attached to the cranium by the forked, posttemporal bone (Pl. 8, A and B). The posttemporal is a curved intramembranous bone which begins to ossify quite early. The dorsal fork is longer and broader than the ventral fork and almost meets its mate from the opposite side at the midline. It is attached to the epiotic by a strong ligament. The spine-like ventral fork is much shorter and smaller and is the posterior ossification of a ligament between the posttemporal and opisthotic. On the dorsal surface of the posttemporal, directly above the ventral fork is a bony tube with 2 or 3 pores which transmits the lateral canal from the extrascapular to the supracleithrum. Ventrally the posttemporal overlaps the supracleithrum.

Supracleithrum. The supracleithrum is a concave intramembranous bone with an acute dorsal thickening which fits under the posttemporal (Pl. 8, B). Just below this, it receives the lateral canal from the posttemporal and transmits it to the lateral line. Ventrally the supracleithrum is somewhat expanded but thinner as it overlaps the cleithrum (Pl. 8).

Cleithrum. The cleithrum is a large, triangular intramembranous bone which comprises a considerable part of the pectoral girdle (Pl. 8). Dorsally, from a point at a level with the middle of the opercle, it curves around beneath the branchiostegal rays and forward to the level of the epihyal bone. It has a fold on its ventrolateral surface, that becomes a thickened ridge which turns inward at the scapular articulation and passes upward on the inner surface of the dorsal arm. Posteriorly the cleithrum overlaps 2 of the 3 postcleithra and, ventrally, it articulates with the scapula. Near the scapular articulation it is braced from beneath by two prongs from the mesocoracoid and by a pendant cleithral flange which joins a flange from the coracoid (Pl. 8, A). The anterior tip of the cleithrum articulates with the forward extension of the coracoid (Pl. 8, B).

Postcleithra. The grayling has 3 postcleithra which arise intramembranously. The first two are similar in size and shape, being thin ovals and more than twice as long as broad (Pl. 8). The first is partly covered by the supracleithrum and cleithrum (Pl. 8, B). Ventrally it narrowly overlaps the second postcleithrum. Posteriorly all three are buried in the skin and appear superficially almost continuous with the scales. The 2nd postcleithrum lies almost wholly beneath the cleithrum, except ventrally where it in turn overlaps the 3rd postcleithrum (Pl. 8, B). The 3rd postcleithrum is quite different from the other two. Less scale-like, it is an arched splint of bone lying in the muscle beneath the pectoral fin (Pl. 8).

SCAPULA. The primary shoulder girdle consists of the scapula, coracoid, and mesocoracoid, all endochondral bones. The scapula lies ventral of the cleithrum to which it articulates (Pl. 8, A). Anteriorly the scapula is separated from the coracoid and the upper two actinosts by a narrow strip of cartilage. The first pectoral ray articulates with the posterior border of the scapula. A mesally directed ridge of bone from its ventral edge articulates with one of the projections on the mesocoracoid. The large scapular foramen lies wholly within the scapula (Pl. 8).

MESOCORACOID. The mesocoracoid is a strongly arched, inverted, U-shaped bone which lies on the mesial surface of the girdle and acts mainly as a brace between the cleithrum and the primary shoulder girdle (Pl. 8, A). The outer arm is narrow and splint-like and lies in intimate contact with the inner wall of the cleithrum, extending downward almost to the cartilaginous edge of the scapula. The inner arm is greatly expanded and longer; it articulates broadly with a mesiodorsal flange from the coracoid and with the inner edge of the scapula. Thus is formed the large mesocoracoid arch (Pl. 8).

CORACOID. The coracoid is keel-shaped with two dorsally directed wings of bone, an inner, meeting the mesocoracoid, and an outer, meeting a flange from the cleithrum (Pl. 8, A). Posteriorly the coracoid is separated from the scapula by a narrow strip of cartilage below which a pointed posterior process extends backward (Pl. 8). The coracoid extends forward beneath the cleithrum, its anterior tip turning upward to meet the anterior end of that bone. An oval interosseus space (Starks, 1930) is left separating the coracoid and cleithrum between their two points of union (Pl. 8, A and B).

PECTORAL FIN. Four actinosts are present, the upper two articulating with the scapula and the lower two with a triangular piece of cartilage lying between the coracoid and scapula. The upper is the smallest; the others become progressively longer ventrally (Pl. 8, A and B). There are 15 to 17 pectoral rays. The uppermost ray is longest and heaviest, and articulates directly with the scapula. The remainder become progressively smaller, ventrally, and articulate with the actinosts.

PELVIC GIRDLE

The pelvic girdle consists of a pair of L-shaped bones, the basipterygia (Pl. 7, D). The foot of the L is situated posteriorly and directed medially, meeting its mate from the opposite side in a cartilaginous articulation at the midline. The longer, anteriorly-directed arm meets its fellow at the midline in a knob of cartilage. Thus the pair encloses a large interosseous triangle (Pl. 7, D). On the posterior surface of each basipterygium there is a small ossification (pterygiophore) lying between the basipterygium and the most medial fin ray. The rays are paired, each forking on either side of the basipterygium, on the outer curved portion of which they articulate. There are usually 11 rays in the pelvic fin, of which 9 or 10 are branched; the outer 1 or 2 are short and simple. An axillary process or modified scale lies along the outer angle of the pelvic fin.

OSTEOLOGY OF THE WHITEFISHES (COREGONINAE)

The whitefishes may be separated from other salmonid fishes by the presence of a well-ossified hypethmoid bone and the lack of teeth on the maxillae at any stage in life. Three genera may be recognized in this subfamily: *Prosopium*, *Stenodus*, and *Coregonus*. *Prosopium* is distinguished from the other two by a single flap between the nostrils (two in *Coregonus* and *Stenodus*), an ossified basibranchial plate (Pl. 6, A) superimposed over the median basibranchial bones (also present in the Salmoninae but absent in *Stenodus*, *Coregonus*, and *Thymallus*), and, in so far as is known, parr marks on the juveniles. *Prosopium* includes 6 species: *cylindraceum*, *williamsoni*, *spilonotus*, *abyssicola*, *coulteri*, and *gemmiferum*. Of these, the first inhabits eastern Asia and northern North America, the others all live in western North America and *P. coulteri* also occurs in Lake Superior.

Stenodus is characterized by having a closed orbital ring (supraorbital one meets the dermosphenotic above the orbit), a large, well-toothed mouth in the adult, and large, heavy bones. There is a single species, *S. leucichthys*, inhabiting the Caspian region, eastern Asia and northwestern North America.

In *Coregonus* there are two internarial flaps, no ossified basibranchial plate, the orbital ring is open dorsally, the mouth is small to moderate in size with weak to moderate dentition, and parr marks are never present. Differences in structure and position of mouth, body form, and number and length of gill rakers have been used by some authors to separate some species as a genus (*Leucichthys* or *Argyrosomus*) distinct from *Coregonus*. These characters are subject to broad intergradation and overlap among species (e.g., Svärdson, 1957). Similar modifications have evolved independently in *Prosopium* as apparent adaptations to feeding behavior, and those in *Coregonus* may well have developed repeatedly (Drs Bailey and Eschmeyer, personal communication). I did not find any distinctive morphological differences and thus *Leucichthys* is regarded as unacceptable and is placed in the synonymy of *Coregonus*. The species of *Coregonus* range throughout northern Europe and Asia and northern and northeastern North America. The number of species to be recognized in *Coregonus* is a subject for debate. Berg (1948) listed 11 from Russia alone but Svärdson (1957) believes there are only 7 in the entire Palearctic. Five species are endemic to the Great Lakes (*alpenae*, *hoyi*, *johannae*, *kiyi*, and *reighardi*) and 5 additional species (*artedii*, *clupeaformis*, *nigripinnis*, *nipigon*, and *zenithicus*) inhabit those waters but occur, or are thought to occur, elsewhere to the northwest. Four other species *sardinella* = *albula* (Svärdson, 1957), *autumnalis* = *oxyrhynchus* (Svärdson, 1957), *nasus*, and *pidschian* are known from northwestern North America but all of these occur also in Siberia and two are perhaps conspecific with species living in the Great Lakes, as suggested by Svärdson (1957). The remaining species *lavaretus*, *peled* and *baunti* inhabit northern Europe and Asia. If Svärdson's estimate of the number of Old World species is correct, there may be as few as 15 species of *Coregonus*, probably not more than 17.

Only adult specimens of *Stenodus* were available. All data on *Prosopium* were obtained from preserved material; all six species were used in making the comparisons. Species of *Coregonus* were more readily accessible in both fresh and preserved state (Table I).

The Chondrocranium

The Olfactory Region

The general shape of the coregonine olfactory region is similar to that of the grayling, there being a bluntly rounded rostrum and two lateral horns forming the margin of the nasal cup. The region also is greatly expanded in width, posteriorly, as it flares out into the prefrontals. However, the prefrontals are directed forward, especially in *Coregonus artedii* (Pl. 3, A) rather than at right angles to the ethmoid cartilage, as in the grayling (Pl. 1, A). The primary distinction is in the endochondral ossification, the hypethmoid lies dorsally between the nasal capsules so that in the coregonine fishes the cartilaginous nasal capsule is partly ossified (Pl. 3, A). A further difference is noted in *Prosopium cylindraceum*, *P. abyssicola*, *P. williamsoni*, *Coregonus nasus*, and to a less extent in *C. clupeaformis*, in which the rostrum curves ventrally. The whole anterior ethmoid region is rounded so that the rostral horns lie ventral to the nasal capsules. Berg (1940: 426) stated that the hypethmoid of *Stenodus leucichthys* is a thin round plate which does not penetrate deep into the cartilage. My observations indicate the only difference to be that in *Stenodus* the dorsal plate is rounded, rather than rectangular or bifurcated as in other coregonines.

The Orbital Region

As in the grayling, much of the orbital region in the Coregoninae has been eliminated. Three bones comprise the orbital region, the orbitosphenoid, a pair of pterosphenoids, and the basisphenoid. The orbitosphenoid, which is absent in the grayling, is a small wing-shaped endochondral bone in *Prosopium* and *Coregonus*, but is large and heavy in *Stenodus*. It lies in the sagittal plane and forms part of the dorsal interorbital septum. The orbitosphenoid is surrounded by cartilage, except posteriorly where it meets the pterosphenoid. The pterosphenoids form part of the posterior wall of the orbit, then extend dorsally to form part of the rim of the dorsal fontanelles (Pl. 3, A). The small Y-shaped basisphenoid touches the prootics on either side with the leg extending anteroventrally to connect to the parasphenoid by a band of cartilage. The basisphenoid is poorly developed in the coregonine fishes. It is much smaller than in the grayling and is often incompletely ossified. It is difficult to find and is most readily located in stained specimens. It was not located in all specimens; thus it may have been overlooked or at times it may fail to ossify. However, a basisphenoid was found in some specimens of *Coregonus artedii*, *C. hoyi*, *C. clupeaformis*, *Prosopium cylindraceum*, *P. gemmiferum*, *P. williamsoni*, and *Stenodus leucichthys*. The basisphenoid may be present or absent in the coregonines (Berg, 1940: 426).

The Otic Region

All 8 bones (6 are paired) found in the otic region of the grayling are present in the chondrocranium of the coregonines, and marked similarity in form and position is observed throughout. These 8 bones are the paired sphenotics (Pl. 3, A), prootics, pterotics, epiotics, opisthotics, and exoccipitals. The median bones are the supraoccipital (Pl. 3, A) and the basioccipital. The opisthotic is present in all coregonines; it rests loosely at the junction of the exoccipital, pterotic, and epiotic (Pl. 3, A). The supraoccipital is a rounded median bone and, except for its posteriorly directed spine, is almost completely covered by the parietals. The curved exoccipital forms part of the posterior and lateral wall of the chondrocranium. It is the only bone in contact with the foramen magnum. The main articulation for the first vertebra is the basioccipital, which then extends forward beneath the chondrocranium to meet the prootic.

Three otoliths are present in the coregonines but only the largest, the sagitta, was studied. As in the grayling, it lies in a vault on the floor of the basioccipital, with the anterior rostrum pointing toward the prootic. The sagitta is similar among the coregonines examined and is much like that of the grayling (Pl. 16).

Investing Bones

Dorsal Roofing Bones

The head of the Coregoninae is not so completely overlain with dermal bone as is that of the grayling; the bones are thinner and more transparent (except in *Stenodus*). All dorsal roofing bones present in the grayling also are present in the coregonines and some, such as the paired nasal and pterotic and the median supraoccipital crest, do not show sufficiently important differences to be contrasted.

The dorsal roofing bones of the coregonines form a rather acute angle, anteriorly (Pl. 9, C). Thus, the supraethmoid and premaxillae (except in *Stenodus*) are small and narrow. The supraethmoid covers the ethmoid cartilage and at least part of the hypethmoid. In those species with subterminal mouths (*Coregonus clupeaformis*, *C. nasus*, *Prosopium abyssicola*, *P. cylindraceum*, *P. spilonotus*, and *P. williamsoni*) the supraethmoid overlaps only a small portion of the anterior end of the hypethmoid. In the above species, it appears that the supraethmoid follows the rounded curvature of the snout while the hypethmoid remains stationary. Since the supraethmoid appears to have moved forward around the snout, it is not in contact with the frontals as in *Stenodus leucichthys*, *Prosopium gemmiferum*, *Coregonus sardinella*, *C. artedii*, and similar forms with terminal mouths. Anteriorly the supraethmoid forms a nearly straight suture with the premaxillae at the midline (except in *Coregonus clupeaformis* and *C. nasus*). In these two species, the supraethmoid has a median, vertical ridge of bone at its pointed anterior end. This is similar to that illustrated by Berg (1940: 237) for *Coregonus lavaretus*, but the position is somewhat different since the supraethmoid lies anterior of the hypethmoid in *C. clupeaformis* rather than over it, as is shown for *C. lavaretus*. Of the dorsal roofing bones, the supraethmoid

shows the greatest diversity among the coregonine fishes. In *Stenodus leucichthys*, this bone is large, but it is thin, flat, and digitate posteriorly (Pl. 11). The closest approach to this type in other coregonine species is found in *Coregonus artedii* and allied species, in which it is much smaller but is thin, flat and somewhat emarginate posteriorly (Pl. 12, B). In *Prosopium* (except *P. gemmiferum*) the supraethmoid is somewhat concave and with very few irregularities at either end (Pl. 12, C and D). It is proportionately longer, being about 3 times as long as wide, as compared with the 2 to 1 ratio found in *Coregonus*. In *Prosopium gemmiferum*, the supraethmoid is long, narrow and covers much of the underlying hypethmoid bone (Pl. 12, G) and although it is a larger bone it is not much different in appearance from that of *P. abyssicola* (Pl. 12, D). Its greatest length-to-width ratio is about 4 to 1, thus confirming the interpretation of affinity with *Prosopium* rather than *Coregonus*. The supraethmoid of *Coregonus nasus* and *C. clupeaformis* (Pl. 12, A) is also distinctive. It is triangular, with 3 posteriorly directed points and the length-to-width ratio is about 2 to 1. It probably indicates an independent evolutionary line from *Prosopium*, although both genera have curved snouts and inferior mouths. In *Coregonus sardinella*, the posterior margin of the supraethmoid (Pl. 12, E) is not deeply notched as in *C. artedii* (Pl. 12, B), *C. kiyi*, *C. reighardi* and related forms. However, it is rather broad and flat as it is in these species.

As in the grayling, the frontals of the coregonine fishes are large subtriangular bones covering most of the dorsal surface of the chondrocranium (Pl. 9, C). In *Stenodus leucichthys*, supraorbital 1 meets the long, anteriorly-directed dermosphenotic, preventing the frontal from being exposed on the dorsal rim of the orbit. The exclusion of the frontal from the orbital rim is approached in *Coregonus*; the condition differs among its various species, but the frontal forms about 10 to 15% of the circumference of the orbit. In species of *Prosopium*, the frontal occupies about 20 to 25% of the orbital rim, and *Thymallus arcticus* is intermediate, with a break of about 17% of the orbital ring. Most of the posterior margin of the frontals overlaps the parietals. The frontals meet at the midline, posteriorly, but gradually separate toward the snout. The frontal in *Coregonus artedii* and in *Stenodus leucichthys* is a rather long, tapered bone whereas that of *Prosopium cylindraceum* and of *P. williamsoni* is somewhat rounded laterally, shorter and comes abruptly to a point anteriorly. In *Coregonus clupeaformis* and *Prosopium gemmiferum* the frontals are somewhat intermediate between these two shapes.

The parietals are irregularly-shaped bones which usually cover a small part of the dorsal fontanelles and much of the supraoccipital. The posterior margins of the parietals are hidden by the dorsal extrascapular bones (Pl. 9, C). The parietals meet in the midline to some extent, except in *Stenodus leucichthys*, in which they are narrowly in contact or are close to the midline and are not pushed aside as in the salmonines. The parietal suture is most apparent in the species of *Prosopium*; in *Coregonus clupeaformis*, the parietals are slightly separated for most of their length.

Posterior of the parietals two pairs of extrascapular bones lie across the rear margin of the skull. They are tubular and bear the supratemporal canal. The

more lateral extrascapular is the larger, being somewhat expanded posteriorly, and bears a triradiate canal. It receives two canals, the lateral canal from the pterotic and the supratemporal canal from the dorsal extrascapular, which unite and continue to the posttemporal. The more dorsal extrascapular is smaller and more slender than the other. It meets its mate from the opposite side but does not cross the midline as in *Thymallus arcticus*. The paired extrascapulars are quite stable throughout the coregionines. Two individual variations were found in *Prosopium cylindraceum*; in each specimen a third, small pair of extrascapulars was found between the other two.

Other dermal bones seen from a dorsal aspect are the premaxillae, supraorbitals, dermosphenotics, pterotics, posttemporals, and supraoccipital. The first three are discussed with the lateral skull bones. The posttemporal is part of the pectoral girdle. The pterotics and supraoccipital are of mixed derivation. Only their dermal portions are pertinent here, and these have been mentioned.

Lateral Skull Bones

The lateral surface of the head of the coregonine fishes is fairly well invested with bone, except for areas around the orbit, between the postorbitals and preopercle, and above and below the pterotic (Pl. 10, A).

In some species (e.g. *Coregonus clupeaformis*, *Prosopium coulteri*, and *P. cylindraceum*) the premaxillae project; in *Prosopium gemmiferum*, *Coregonus artedii* and some others, they are about equal with the dentary; whereas in *Stenodus leucichthys* and *Coregonus alpenae* they do not extend forward as far as the dentary.

The coregonine premaxilla is a small, thin bone which meets the supraethmoid dorsally, the maxilla laterally, and its mate at the midline. In specimens of *Prosopium coulteri*, *P. cylindraceum*, *Coregonus artedii*, and *C. clupeaformis* 30 to 40 mm total length, 6 to 8 small but well-developed teeth are present. Even in later stages (73 to 84 mm total length) teeth were still clearly evident. In the adult of *Coregonus artedii* an occasional small, weak tooth may be found. A few teeth are always present on the premaxilla of the adult of *Stenodus leucichthys* (Pl. 13, F), although it is a small, narrow bone contributing little to the margin of the gape. In *Coregonus clupeaformis*, *Prosopium cylindraceum*, (Pl. 13, E) *P. coulteri*, and *P. spilonotus*, the premaxilla is an almost vertical plate at the end of the snout, its height subequal to its length. In *Coregonus artedii* and *C. sardinella* (Pl. 13, G), the premaxilla extends so far laterally that its horizontal length is about twice its height.

The coregonine maxilla is a distinctive bone (Pl. 10, A). Instead of being long, narrow and toothed as in the salmonines and thymallines, it is short, broad and curved much like the runner on a sleigh (Pl. 13, A, B, E-G). The outstanding feature, however, is the absence of teeth at any stage of development. The maxilla also displays notable variation in shape among the whitefishes (Gąsowska, 1960). In *Prosopium abyssicola*, *P. cylindraceum* (Pl. 13, E), *Coregonus clupeaformis*, and *C. nasus* (Pl. 13, A) it is S-shaped and the posterior

half is expanded. When the mouth is open, it is the middle one-third which is exposed at the margin of the gape. In *Prosopium gemmiferum* (Pl. 13, B), *Coregonus artedii*, *C. sardinella*, (Pl. 13, G) and *Stenodus leucichthys* (Pl. 13, F) the maxilla is about equally expanded throughout (except the rounded knob which articulates with the palatine) and the anterior two-thirds borders the gape when the mouth is open.

An anterior depression in the ventral margin of the maxilla, that forms the articulating surface for the premaxilla, is balanced in the rear by a dorsal depression which receives the supramaxilla. The supramaxilla is quite characteristic in the coregonine fishes, but in all there is a severely attenuate anterior projection. This is quite different from the supramaxilla in other salmonid fishes, in which this bone is a simple, lanceolate structure (Pl. 13, C-D, and H).

The first supraorbital bone is much larger in *Coregonus artedii*, *C. clupeaformis*, and *Stenodus leucichthys* than in the grayling. In these 3 species, the first supraorbital is one-third to one-half the length of the frontal, but in the grayling it is always less than one-third the frontal length. In *Prosopium* it is a small bone, as in the grayling. The greatest development is shown in *Stenodus leucichthys*, in which the supraorbital extends backward until it touches the dermosphenotic, eliminating the frontal from the rim of the orbit.

The second supraorbital is a narrow, curved bone that is much smaller than the first and not so strongly arched as in the grayling. It has a broad ventral suture with the lachrymal but it barely makes contact by a dorsally upturned point with supraorbital one.

The lachrymal, 3rd in the series of circumorbital bones, is thin, more or less triangular, and bears the anterior terminus of the infraorbital canal. The anterior end of the lachrymal is bluntly rounded, more so in *Stenodus leucichthys* than in any other coregonine. Posteriorly it meets the infraorbital, which exhibits little difference among the various species studied.

There are 3 postorbital bones in all species of coregonines studied. The first is somewhat narrower anteriorly where it meets the infraorbital, and widens dorsally at its suture with the 2nd postorbital. Postorbital 3 articulates with the dermosphenotic. All three carry the infraorbital canal. In all but *Stenodus leucichthys*, the 3rd postorbital is widest; but in that species the 2nd is the broadest. Also, in *Stenodus* the postorbitals fail by a considerable space to extend to the preopercle. In species of *Prosopium*, only the 3rd postorbital comes in contact with the preopercle. In *Coregonus*, the 3rd and usually a part of the 2nd postorbital are in narrow contact with the preopercle (Pl. 10, A).

The dermosphenotic is the 8th circumorbital bone in the coregonine fishes. Like the grayling, it bears a triradiate sensory canal. It lies over the sphenotic, articulates with postorbital 3 ventrally, with the frontal dorsally (except in *Stenodus*) and with the pterotic laterally. The dermosphenotic forms part of the posterodorsal rim of the orbit. In *Stenodus* the bone is produced anteriorly and contributes a larger share to the orbital rim; it meets the 1st supraorbital to close the circumorbital ring.

The V-shaped dentary is a concave bone forming the greater part of the lower jaw. Anteriorly it curves inward to meet the dentary of the opposite side in a loose, easily separable symphysis. The longer lower arm of the V is almost straight along its ventral surface and bears the mandibular canal. At its posterior tip, it just touches the small retroarticular, and the angular fits between the two arms of the V. The dorsal arm of the V is wing-shaped and gives the coregonine dentary its characteristic shape, which is readily distinguishable from the grayling's dentary. The anterodorsal slope of this wing is rather abrupt in small-mouthed species (*Coregonus clupeaformis*, *C. nasus*, *Prosopium coulteri*, *P. cylindraceum*, and *P. williamsoni*), more gradual in the larger-mouthed forms (*Coregonus artedii*, *C. hoyi*, *C. kiyi*, *Prosopium gemmiferum*, and *Stenodus leucichthys*). The inner concavity of the dentary receives the anterior tip of Meckel's cartilage. Although teeth are borne on the dentaries of the juveniles of all species studied (to a length of approximately 80 mm), only *Stenodus leucichthys* bears teeth as an adult, and these are few and weak (Pl. 11). Berg (1940: 426) mentioned that a small inframandibular bone is present on the dorsal wing of the dentary in *Stenodus leucichthys*. However, this bone was not noted in the specimens of *Stenodus* used in this study (Pl. 11). Dineen and Stokely (1954) pointed out that the inframandibular bone is not a constant feature in *Umbra limi*, a characteristic which may apply also to *Stenodus*.

Except for the posterior articular portion, most of the coregonine angular is a thin transparent bone fitting into the V-shaped notch in the dentary. Its posterodorsal surface has a curved notch to receive the rounded knob of the quadrate. Just below this notch a tubular bone has fused to the angular, providing a connection from the preopercular to the mandibular canal. Ventral to the canal, there is an irregular suture with the retroarticular. The inner posterior surface of the angular is well ossified around Meckel's cartilage. The mandibular portion of the adductor mandibularis muscle is firmly inserted along the mesal surface of Meckel's cartilage, as well as on the coronomeckelian. The angular of *Coregonus artedii* and *Prosopium gemmiferum* is long and pointed, anteriorly, much like that of *Thymallus arcticus*, In *Stenodus* the angular is rounded anteriorly, and in *Coregonus clupeaformis*, *Prosopium cylindraceum* and *P. williamsoni* it is pyramidal in form with an S-shaped curve in front.

The retroarticular, a small triangular bone at the posteroventral corner of the angular, is little differentiated among the species studied and is similar to the retroarticular of the grayling, except that it is slightly larger and is not firmly fused to the angular. All of the coregonine fishes studied possess a coronomeckelian lying partly over Meckel's cartilage and fused to the angular.

The coregonine preopercle is a strongly arched bone, similar to that of the grayling. The vertical arm is about 1½ times the length of the horizontal arm and carries the sensory canal directly to the pterotic, where it joins the lateral temporal canal. No suprapreopercular bone is present in any of the Coregoninae (Pl. 10, A).

Paired opercles, subopercles, and interopercles are present but no significant differences were noted among the various species of coregonines studied.

The branchiostegal rays lie in a series on the ventral surface of the head, each overlapped by the one next behind. The first 5, 6, or 7 rays are attached to the ceratohyal; the remainder to the epihyal bone. The number of branchiostegal rays varies from 6 to 11. *Coregonus artedii*, *C. hoyi*, *C. kiyi*, *Prosopium gemmiferum* and *P. williamsoni* have 7 to 9 branchiostegals; *C. clupeaformis* has 8 to 10; *P. coulteri* has 7 or 8 and *P. cylindraceum* has 6 to 8. *Stenodus leucichthys* has 10 or 11 branchiostegal rays, the largest number in the Coregoninae.

Ventral Bones of Cranium

The vomer in the coregonines is a thin, rounded bone lying on the ventral surface of the ethmoid. In *Stenodus leucichthys* it is well developed and the head bears numerous small teeth (Pl. 11). It narrows posteriorly, to a point which overlaps the parasphenoid. In *Coregonus artedii* and *C. clupeaformis*, the vomer is smaller and has a few vestigial teeth only in the young. It is widest anteriorly, does not extend far back, and terminates in a blunt tip. In the species of *Prosopium*, the vomer is poorly developed; there remains a small oval ossification and a short shaft which barely touches the parasphenoid. No teeth were observed. Except in *Stenodus*, the vomer of the coregonine fishes is less well developed than in *Thymallus*.

The parasphenoid extends almost the entire length of the chondrocranium, from the lateral horns of the rostrum to the rear end of the basioccipital. In all species it is overlapped anteriorly by the vomer, but to a greater extent in *Coregonus artedii*, *C. clupeaformis*, and *Stenodus leucichthys*. Just behind the orbit, two wings from the parasphenoid extend dorsally to meet the basioccipital and enclose the posterior myodome. This chamber for the eye muscles is open posteriorly in all the coregonines. In *Coregonus artedii*, the parasphenoid is fairly straight until it reaches the otic region and then bends dorsally, the two parts forming an angle of about 160°. This is similar to but less abruptly bent than that of the grayling, which has an angle of about 140°, and *C. clupeaformis* with about 150°. In *Prosopium cylindraceum*, the bending is still less pronounced (about 170°), and in *Stenodus* the ventral contour of the parasphenoid is straight (approximately 180°).

Visceral Arches

Palatoquadrate Arch

The palatine in the Coregoninae is rather short and lies in front of the ectopterygoid. The anterior endochondral portion is cylindrical and thus is well differentiated from the posterior dermal portion. The palatine articulates at two points with the ethmoid cartilage, the first beneath the anterior tip of the maxilla and the second a short distance posterior. The second articulating surface is particularly well developed in the coregonines, ending in a rounded, well-ossified cylinder. Beyond this point, the palatine becomes much reduced in size and ends rather abruptly, especially so in the species of *Prosopium*. Weak, small teeth are borne on the palatine during the young stages of all coregonines

studied, but they are lost as juveniles, except in *Stenodus leucichthys* and *Coregonus sardinella*. In adults of *Stenodus* there are many small teeth in a broad band that is continuous with the vomerine tooth patch (Pl. 11).

Paired ectopterygoids, quadrates, metapterygoids, and mesopterygoids are present in all coregonines. The mesopterygoid is never toothed in the coregonines.

Hyoid Arch

The hyomandibular of the coregonines is similar in shape to that described for *Thymallus arcticus*. Among the coregonines, the hyomandibular of *Stenodus leucichthys* shows the greatest divergence. The bone is relatively shorter than in other species and the opercular condyle is somewhat longer.

The symplectic acts as a connecting rod of bone between the quadrate, hyomandibular, and metapterygoid. The interhyal articulates at the cartilaginous junction of the symplectic with the hyomandibular. There is little difference among the symplectics of the various species studied.

The description of the interhyals, epihyals, ceratohyals, and hypohyals of the grayling suffices for the coregonines, as there is little distinctive about these bones in the subfamily. Two or 3 branchiostegal rays are borne on the epihyal, the remainder on the ceratohyal.

The basihyal is cartilaginous and covered with a lingual plate. In the grayling the lingual plate is spatula-shaped, with a patch of teeth in the centre (Pl. 6, C). However, in *Coregonus artedii* and *C. sardinella* the lingual plate is long and thin with weak teeth scattered along the length of the bone. In *Stenodus leucichthys* it is of similar shape but fairly bristles with tiny teeth and overlaps the first basibranchial. The lingual plate of *Coregonus clupeaformis* and *C. nasus* is oval and many small teeth are scattered over the dorsal surface. It overlaps the first basibranchial bone in *C. nasus* but not in *C. clupeaformis* (Pl. 6, D). The lingual plate is more variable in *Prosopium*. In *P. coulteri* and *P. gemmiferum* it does not touch the first basibranchial. A well-developed central patch of teeth is present on the oval lingual plate of *P. coulteri*, but teeth are absent from the somewhat longer bone of *P. gemmiferum*. In *P. abyssicola*, *P. spilonotus*, *P. cylindraceum*, and *P. williamsoni* a small central patch of teeth is present and the lingual plate touches the first basibranchial. In the first two of these 4 species the shape is ovate; in the last two it is elongate (Pl. 6, A).

Branchial Arches

Three pairs of ossified pharyngobranchials are present in the coregonines, the first of which articulates with the parasphenoid. As in the grayling, they articulate with each other and with the epibranchials. One to 4 small gill rakers usually are present on the anterior edge of the 2nd and 3rd pharyngobranchials. A pharyngeal plate lies over the 3rd pharyngobranchial. It is small and bears a few weak teeth in *Coregonus and Prosopium* (Pl. 6, A and D). It is larger and the teeth are well developed in *Stenodus*.

Four pairs of epibranchials are present. The 4th is atypical, with a round

expanded posterior portion which is partially covered by a 2nd pharyngeal plate. The 2nd plate lies on the dorsal surface of the epibranchial near its junction with the pharyngobranchial, and bears a cluster of tiny teeth (Pl. 6, A and D). Gill rakers are found on the anterior edge of all 4 epibranchials and also on the posterior edge of the first 3.

There are 5 pairs of ceratobranchials. The 5th is somewhat expanded and bears a 3rd, toothed pharyngeal plate (Pl. 6, A and D). As in the grayling, gill rakers are borne on the anterior surface of all 5 bones and on the posterior edge of the first 4. The rakers on the posterior side of the 1st ceratobranchial in *Stenodus* are few and tiny.

Three pairs of hypobranchials, similar to those in the grayling connect the ceratobranchials with the basibranchials. The first 2 hypobranchials bear gill rakers on both anterior and posterior surfaces; the 3rd is cone-shaped and bears rakers on only the anterior side in *Coregonus* and *Stenodus*. All species of *Prosopium* (including *gemmiferum*) are like *Thymallus arcticus* in having rakers on only the anterior edge of the hypobranchials.

There are 4 basibranchial bones which lie in a series and are separated by cartilage, although the cartilaginous bridge between the 1st and 2nd is very narrow. The 1st basibranchial is shorter than the others and is triangular. It articulates with the basihyal anteriorly. In *Prosopium*, a single, long, narrow basibranchial plate is present, lying over the dorsal surface of the posterior half of the 2nd basibranchial and extending backward to above the anterior half of the 4th basibranchial (Pl. 6, A). As in *Salmo trutta caspius* (Tchernavin, 1938b), it is fused to the 3rd basibranchial. The basibranchial plate is not present in the grayling, in *Stenodus*, or in any of the species of *Coregonus* examined. It is present in *Prosopium abyssicola*, *P. coulteri*, *P. cylindraceum*, *P. gemmiferum*, *P. spilonotus*, and *P. williamsoni*.

The branchial skeleton of *Stenodus leucichthys* is more dentigerous than that of the other coregonines. Minute teeth are found embedded in the skin over all 3 pairs of pharyngobranchials, on the 4 pairs of epibranchials and along the entire length of both the anterior and the posterior copula. Teeth also are attached to the dermal plates (the lingual and the 3 pairs of pharyngeal plates).

Urohyal

A urohyal bone is present in all coregonines but it is not particularly distinctive. It is rather flat, ventrally, with a dorsal crest as in the grayling.

Axial Skeleton

Vertebral Column

The vertebral column of the whitefishes ranges from a low of 52 vertebrae in *Prosopium coulteri*, to a high of 69 vertebrae in *Stenodus leucichthys* (Koelz, 1929: 321; Eschmeyer and Bailey, 1955: 172; Fuller, 1955: 771). The vertebrae have essentially the same shape as in the grayling. They are largest in the median part of the trunk, becoming progressively smaller anteriorly and posteriorly.

The neural arches are prolonged dorsally into neural spines. The anterior spines are separated to a point below the dorsal fin. They then fuse into sharp spines which slant backward toward the caudal fin. The last 2 or 3 neural spines are expanded. Epineurals are borne on the lateral surfaces of the first 28 to 38 neural arches, the lower numbers being found in species with fewer vertebrae. Occasionally the atlas does not bear an epineural. Anteriorly the neural arches are recessed in pits in the middle part of the centrum, but behind the dorsal fin they are fused to the anterior part of the centrum. Ventrolaterally, pairs of transverse processes are set into pits in the centra. The pleural ribs articulate with the outer surface of the transverse processes. Beyond the dorsal fin, the transverse processes gradually become smaller and fuse to the centra. As in the grayling, the transverse processes of the posterior 7 or 8 trunk (precaudal) vertebrae are longer and slant backward, and the final 2 or 3 are fused across the midline to form a haemal canal. The 1st vertebra does not have ribs but the remaining trunk vertebrae bear pairs of pleural ribs. Those belonging to the precaudal vertebrae do not have articular surfaces but rather adhere tightly to the posterior surface of the transverse processes. The last 20 to 24 caudal vertebrae bear posteriorly directed haemal spines, and the final 3 or 4 of these are broad and flat. Epipleurals, such as are present in the grayling were not observed in any of the Coregoninae.

The caudal fin of the whitefishes is like that of the grayling, with 3 upturned vertebrae and a cartilaginous urostyle. The neural spine of the 4th vertebra from the last, slants sharply backward and looks very much like an epural, similar to the same condition in the grayling (Pl. 14, G and H). It is not fused to its neural arch as are the more anterior neural spines. Two epurals (3, if the detached neural spine from the 4th last vertebra be included) are present in all the coregonines observed. Three pairs of uroneurals are present. The 1st (most anterior) uroneural is a large plate-like structure extending over the last 3 or 4 vertebrae and onto the urostyle. As in the grayling, it has only a small dorsal crest (Pl. 14, G and H). The 2nd lies dorsolaterally of the 1st, partly covering the 1st uroneural and the urostyle. The 3rd and smallest lies beside the second uroneural but extends more posteriorly. The coregonines have 7 hypurals in the caudal fin. Like that in the grayling, the 2nd hypural is the largest. The urostyle curves sharply dorsad and ends between the paired bases of the caudal rays (Pl. 14, G and H). Although the urostyle is chiefly cartilaginous, 1 or 2 nodules of bone may be present.

The principal rays of the caudal fin are typically 19 (17 branched) in number in all the whitefishes studied.

Median Fins

The dorsal fin of the whitefishes is very similar to that of the grayling, except that the rays are fewer. The anterior 2 to 4 rays are unbranched, the remainder are branched but the rays are shorter. All are supported by a series of 3 pterygiophores, exactly as described for the grayling. The insertion of the most

anterior pterygiophore is somewhat variable; it may be anywhere behind the neural spine of any vertebra from 12 to 17. This variation is true of all coregonines except *Stenodus*, in which the dorsal fin is located somewhat posteriorly, and the 1st pterygiophore lies behind vertebra 20, 21, or 22. From 12 to 16 flat interneurals lie in the muscle anteriorly of the dorsal fin. The largest of this series is borne just behind the skull and the smallest is next to the dorsal fin.

The number of dorsal rays is quite variable, between 10 and 15, and is not a particularly valuable taxonomic character in the whitefishes. This figure is somewhat higher than that reported by Koelz (1929) who counted a low of 7 rays in *C. hoyi*, but Eschmeyer and Bailey (1955: 163) pointed out that Koelz did not count the short, anterior unbranched rays. Minimum figures usually are characteristic of *Prosopium coulteri* and maximum counts most often are encountered in *Stenodus leucichthys*. Therefore, the dorsal ray count of *Stenodus* most closely approaches, but does not reach, the minimum number (17) in *Thymallus*.

The coregonine anal fin is basically similar to the dorsal fin. The insertion of the anterior pterygiophore again is variable, and may lie from between vertebrae 29 and 30 to between 42 and 43. The lower figure is that found in *Prosopium coulteri*, while the larger is characteristic of *P. cylindraceum* and *Stenodus leucichthys*, but there is overlap between these extremes. The number of anal fin rays varies from 11 to 16. Again, this figure is higher than that given by Koelz (1929) who omitted short rays from his counts. The higher count is characteristic of *Stenodus*, whereas several species (*Coregonus artedii*, *C. alpenae*, and *P. coulteri*) may have as few as 11 anal rays.

Appendicular Skeleton

Pectoral Girdle

As in the grayling, the posttemporal bone in the Coregoninae connects the pectoral girdle to the dorsal part of the skull at two points, one with the epiotic and the other with the opisthotic bone. The ventral portion of the posttemporal is more expanded than in *Thymallus*. The supracleithrum is the 2nd bone of the series and transmits the lateral canal to the lateral line. Ventrally, the supracleithrum overlaps the cleithrum and 1st postcleithrum. The whitefish cleithrum, like that of the grayling, is the largest bone of the pectoral girdle and extends far forward beneath the pharynx.

Three postcleithra are present in all the coregonines studied. Berg (1940) stated that *Stenodus leucichthys* has only 2 postcleithra, but 3 were found in each of the 8 specimens examined (Pl. 11). The 3rd postcleithrum is small and rounded, in contrast to the long, narrow, splint-like bone in other coregonines. It seems clear that the 3rd postcleithrum was overlooked by Berg. The oval 1st postcleithrum lies below the angular junction of the supracleithrum and cleithrum and is overlapped by these 2 bones. There is a moderate gap of variable width between the 1st and 2nd postcleithrum in *Stenodus* (Pl. 11) and

in *Coregonus*, and a narrow space between them in *Prosopium*, but these 2 postcleithra are in contact in the grayling (Pl. 8, A). The 2nd postcleithrum is the largest bone of the series and is almost completely covered by the posterior expansion of the cleithrum, which in turn overlaps the 3rd postcleithrum. The latter is a narrow bone, somewhat expanded dorsally but most often coming to a sharp point ventrally. It is subject to individual variation and often is quite blunt and oblong in *Coregonus artedii*, and it is round or oval in *Stenodus* (Pl. 11).

The bones of the primary shoulder girdle consist of paired scapulae, mesocoracoids, and coracoids. These in coregonines are similar in shape and position to those described for the grayling. The scapular foramen lies wholly within the scapula, the mesocoracoid is arched, and the coracoid runs forward, and meets the coracoid from the opposite side where they articulate with the cleithra.

Four actinosts are present in all the whitefishes studied. They support all but the 1st pectoral fin ray, which articulates directly with the scapula.

The number of pectoral rays ranges from 13 to 18 among the coregonines (Koelz, 1929: 319), but the number is not distinctive, there being broad overlap among species. *Coregonus artedii*, *C. hoyi*, *C. kiyi* have a relatively high count, 14 to 18 rays, species of *Prosopium* have 13 to 16, and other coregonines have 14 to 18 rays.

Pelvic Girdle

Like the grayling, the whitefish pelvic girdle consists of a pair of L-shaped basiopterygia which meet anteriorly in a rather sharp point. Posteriorly they join at the midline in a cartilaginous suture. The pelvic fin rays range in number from 9 to 13, but their number is of little taxonomic value (Koelz, 1929: 320; Eschmeyer and Bailey, 1955: 170). A well developed axillary process is found in all coregonines.

OSTEOLOGY OF THE TROUTS (SALMONINAE)

The Salmoninae may be distinguished from the other salmonid fishes by the presence of a suprapreopercle bone, the absence of a dermosphenotic bone, and the broad separation of the parietals by the supraoccipital. Five genera may be recognized in the Salmoninae: *Brachymystax* Günther, *Hucho* Günther, *Salvelinus* Richardson, *Salmo* Linnaeus, and *Oncorhynchus* Suckley. A sixth genus, *Salmothymus* Berg (consisting of 2 species from Yugoslavia), is recognized by some authors (Berg, 1932, 1940) but it has been placed in the synonymy of *Salmo* by Regan (1920) and Nall (1930). I have examined a specimen of *S. ohridanus* and see no need for its separation from *Salmo*.

Brachymystax is characterized by the presence of fine teeth on the jaws (Pl. 13, D) (Tchernavin, 1923) and a small mouth; the jaw articulation is located below the eye rather than behind its rear margin as in the other 4 genera. The vomer is small with a short, toothless shaft. A single row of small teeth is continuous from the palatines across the head of the vomer to form an unbroken

oval series on the roof of the mouth (Fig. 1, B). There is a single species, *B. lenok*, which inhabits Siberia and eastern Asia.

Hucho is somewhat intermediate between *Brachymystax* and *Salmo*. As in *Brachymystax*, the shaft of the vomer is short and toothless, and the palatine and vomerine teeth form a continuous U-shaped series on the roof of the mouth (Fig. 1, C). As in Salmo, the jaws bear strong canine teeth (Pl. 13, H) and the jaw articulation is located well behind the eye. *Hucho* inhabits the Danube River, Siberia and eastern Asia (Dymond and Vladykov, 1934).

Salmo is charcterized by well developed teeth on the shaft of the vomer so that the vomerine and the palatine teeth form a T on the roof of the mouth. There is a narrow toothless gap between the palatine teeth and those on the head of the vomer (Fig. 1, E). *Salmo* is further distinguished from *Salvelinus* because it has dark spots present on a lighter background. *Salmo* has a wide but discontinuous distribution, occurring in Europe, in eastern and in western North America, and in eastern Asia (Dymond and Vladykov, 1934).

Salvelinus has light spots present on a dark background and the shaft of the vomer is toothless (Morton and Miller, 1954: 122). There is a gap between the palatine teeth and those on the head of the vomer (Fig. 1, D), in contrast to *Brachymystax* and *Hucho*. *Salvelinus* is widely distributed across northern Europe, Asia, and North America and extends well into the temperate zones in these continents.

Oncorhynchus may be separated from the other genera because in the adult the dorsal fontanelles are grown over with cartilage (Tchernavin, 1938a) and the cartilaginous rostrum is azygous (Tchernavin, 1937: Fig. 2). As in *Salmo*, the shaft of the vomer is toothed, but there is a wide gap between the palatine and vomerine teeth (Fig. 1, F). *Oncorhynchus* is largely confined to the north Pacific Ocean and the area of Asia and North America bordering it; there is limited penetration of the Arctic Ocean from Bering Straits.

Fresh and preserved material of *Salmo* and *Salvelinus* was readily available for this study. As for *Oncorhynchus*, only the heads were available in the fresh state. The remainder of the data for *Oncorhynchus*, as well as for *Hucho* and *Brachymystax* was obtained from preserved specimens (Table II).

The Chondrocranium

The Olfactory Region

The olfactory region of the salmonine chondrocranium is of the same general type as that described for the grayling and whitefishes, but some differences are apparent. A small but well-marked indentation or notch at the anterior end of the ethmoid cartilage (rostrum) of *Salmo gairdneri*, *S. trutta*, and *S. salar*, and the simple, bluntly pointed rostrum in the adult *Oncorhynchus*, are both unlike the modifications found in the grayling and whitefishes. The above difference between *Salmo* and *Oncorhynchus*, figured by Tchernavin (1937: 239; 1938a: 166; 1938b: 362), has been used as a basis for separating *Oncorhynchus* from *Salmo*,

in opposition to Regan's (1914: 407) belief that the salmons and trouts should be united in the single genus *Salmo*. This anterior ethmoid notch is not well developed in *Salvelinus fontinalis* and it is even less noticeable in *Salvelinus namaycush* (Pl. 3, B), in which the ethmoid cartilage is rather broad and blunt as in *Thymallus* (Pl. 1, A and B). Observations made on preserved juveniles of *Oncorhynchus keta*, *O. nerka*, and *O. tshawytscha* (s. l. 70 to 110 mm) indicate that the azygous condition illustrated by Tchernavin (1937, 1938a) is secondary, typical of salmon as they approach sexual maturity in the sea and after they return to freshwater. In the juveniles examined, the rostral cartilage appears bluntly truncate, much as in *Salvelinus namaycush*. The notch at the anterior end of the rostrum, so well developed in *Salmo gairdneri*, is very slight or absent. Thus, the condition observed in the juvenile *Oncorhynchus* appears to be intermediate between the forked rostrum of *Salmo gairdneri* and the simple blunt snout of the adult *Oncorhynchus*.

As in the grayling, the only constant ossification present in the ethmoid cartilage of the salmonines is the paired prefrontals (Pl. 3, B). The hypethmoid, a usual feature in the Coregoninae, is nearly always absent in the Salmoninae. Berg (1940: 425) noted its absence as a characteristic of the subfamily. Tchernavin (1938b: 356) stated that there is no true mesethmoid bone in *Salvelinus*. A small dorsal ossification was observed in 2 specimens of *Salvelinus fontinalis* used in this study. Tchernavin (1938b: 357) reported a similar ossification in 2 specimens of *Salmo trutta* from the Baltic Sea and in 2 specimens of *Salmo trutta caspius* (Kessler). Apparently a partially ossified ethmoid plate sporadically occurs through the subfamily but, due to the scanty study of chondrocranial material, it is only rarely observed or reported.

The Orbital Region

The most conspicuous feature of the orbital region of the salmonines is the large orbitosphenoid bone projecting ventrad into the interorbital septum. The orbitosphenoid has a large foramen in front, through which the olfactory tract passes before continuing anteriorly between the oblique eye muscles, through the cartilage mesial to the prefrontal, and thence to the nasal capsule. As in the grayling, the Y-shaped basisphenoid is also well developed in the salmonines and is supported by a partly ossified projection from the dorsal surface of the parasphenoid. The cartilaginous interorbital septum is better developed in the trouts than in either the whitefishes or the grayling. It is particularly heavy in *Oncorhynchus*, but it is enlarged in old specimens of *Salvelinus namaycush*, *S. malma*, and *Hucho hucho*.

The Otic Region

The Otic region of the chondrocranium is well ossified, especially ventrally and laterally. A large expanse of cartilage remains on the dorsal surface (Pl. 3, B). With few exceptions, this part of the chondrocranium is quite similar among all the salmonid fishes. One difference is the small cap-like opisthotic

covering the junction of the pterotic, epiotic, and exoccipital bones. The opisthotic is somewhat peculiar in *Oncorhynchus* because, ventrally, it has a splinter of bone which projects forward and touches the prootic. This was observed by Tchernavin (1938b: 362) and I found it in both *Oncorhynchus nerka* and *O. keta*, but not in *Salmo* or *Salvelinus*. The sphenotic is particularly well developed in the salmonines, forming a sturdy point of origin for the strong levator arcus muscle. The roof of the otic region is not so well ossified, much of the area being occupied by the dorsal fontanelles and a median (*taenia tecti medialis*, de Beer, 1937) and 2 lateral strips of cartilage (postorbital cartilage from auditory capsule, de Beer, 1937) (Pl. 3, B). Tchernavin (1923) noted that the salmonine supra-occipital does not have an anterior bony extension. However, some ossification continues forward on the cartilaginous bridge between the dorsal fontanelles in some specimens of *Salmo gairdneri*, *Salvelinus fontinalis*, and *S. namaycush*, as in *Thymallus* and *Coregonus*.

A pair of dorsal fontanelles is found in all genera of Salmoninae studied, at least in the young and juveniles, and they are proportionally smaller and more circular than in either the grayling or the whitefishes. Tchernavin (1937: 239; 1938b: 362) used the absence of dorsal fontanelles in *Oncorhynchus* as a character to separate *Oncorhynchus* from *Salmo*. Although the fontanelles are small and circular in *Oncorhynchus*, rather than large and oval as in *Salvelinus* and *Salmo*, they were observed in young specimens of *Oncorhynchus keta* (standard length 95 mm), *O. nerka* (83 and 103 mm), and *O. tshawytscha* (71 and 81 mm). In a hook-jawed adult male of the landlocked phase (kokanee) of *Oncorhynchus nerka* (252 mm), the dorsal fontanelles are present but much reduced in size. These observations were made on specimens which had not migrated to the sea. On larger specimens taken in the Pacific Ocean, cartilage had grown over and completely obliterated the dorsal fontanelles.

As in the graylings and whitefishes, the sagitta is the largest of the 3 otoliths found in the trouts and its position is identical. The otolith of the salmonines is relatively smaller and broader than in either the coregonines or the thymallines (Pl. 16). There appears to be some variation of the otolith among individuals, e.g. the sagitta of *Salmo gairneri* sketched for this study (Pl. 16, Q) looks much like the one figured for *Salmo trutta* by Frost (1925, Pl. XII). The otoliths of *Oncorhynchus keta* and *O. nerka* (Pl. 16, O and P) are more like the other salmonines than is the one of *O. quinnat* (*tshawytscha*) figured by Frost (1925). The salmonid otolith does not appear to have much generic significance.

Investing Bones

Dorsal Roofing Bones

A good description and comparison of the skull bones of the Salmoninae is difficult and never completely satisfactory because of changes which occur at the time of breeding.

In his important contribution "Changes in the Salmon Skull" Tchernavin (1938a: 165) commented: "The skulls of adult migratory *Salmo* and *Oncorhynchus*

are subject to striking changes throughout the whole life of the fish. These changes are so marked that the study of the salmon skull becomes, in fact, a study of its changes. Many characters usually regarded as 'fortuitous variations' or as taxonomic distinctions are found to be features of particular phases of these regular changes." For this reason, special emphasis is here given to juvenile specimens in which modifications are less pronounced. This eliminates, to some extent, differences due primarily to the expansion of cartilage in the adult.

The supraethmoid, present in all salmonines, has the greatest taxonomic significance of all the dorsal roofing bones. It is fimbriate posteriorly with some of the finger-like projections overlapping the frontals. Laterally it borders the nasals but does not fuse or articulate with them. Anteriorly the supraethmoid is rounded or triangular, so that it fits between the backward extensions of the premaxilla without overlapping them. The salmonine supraethmoid is useful in classification because of its variation. One type is the widely divergent V-shaped form characteristic of *Oncorhynchus* (Pl. 12, F). In some large specimens, the posterior notch is so deep that the supraethmoid is almost bisected. Varying degrees of depth in the V-shaped indentation are noted in species of *Salmo*. In freshwater specimens of *Salmo gairdneri* (Pl. 12, K), for example, the supraethmoid is wing-shaped and similar to the grayling. *Salvelinus namaycush* and *Brachymystax lenok* lie at the other extreme. Their supraethmoid is long, narrow and irregular, and lacks the widely diverging arms (Pl. 12, I and J). *Savelinus fontinalis* is similar to but not quite as extreme as the lake trout (Pl. 12, L). Kendall (1919: 80) used the proportional width-to-length measurement of the supraethmoid to separate *S. namaycush* from other chars. *Hucho* is similar to *Salvelinus* but in it the supraethmoid is short and broad (Pl. 12, H).

The frontal is a large, triangular bone covering most of the roof of the chondrocranium, as it does in the grayling and whitefishes. The most obvious difference is in the supraorbital canal, which is transmitted directly to the pterotic. In the trouts, unlike *Thymallus* and the coregonines, the dermosphenotic is absent. In adults of *Oncorhynchus*, the frontals are widely separated at the midline by the growth and expansion of cartilage. This extensive growth of cartilage in maturing *Oncorhynchus* even erodes away the bone so that the frontal is no longer very triangular and comes to a blunt point anteriorly. This divorce of the frontals is foreshadowed even in the young, in which the bones are partly separated by a strip of cartilage. The frontals of other species are more closely articulated at the midline and fusion across the frontals sometimes occurs in *Salvelinus fontinalis*.

The parietals in the salmonines are small rectangular bones that cover a small portion of the skull roof as compared to those of the grayling and whitefishes. They are completely separated by the supraoccipital and lie on the dorsolateral surfaces of the chondrocranium (Pl. 9, B).

In the trouts the extrascapulars are merely tubular bones, carrying the supratemporal canal, and are not expanded as in the whitefishes and grayling. There usually are 4 pairs but 5 or 6 sometimes occur and *Brachymystax* has only 3 pairs. The pair nearest the middle usually meet at the midline as in the

Coregoninae. This character is somewhat variable, however, as *Salvelinus fontinalis* and *S. namaycush* sometimes have a median extrascapular (Pl. 9, B) as is typical in the grayling.

The supraoccipital has become more important as a dorsal roofing bone in the Salmoninae. Not only the occipital crest but also a thin lamina of bone covering the exposed portion is of dermal origin (Pl. 3, B and 9, B).

As in other salmonids, paired nasals are located on either side of the supraethmoid. Paired pterotics, well developed but not particularly distinctive, also are present.

Lateral Skull Bones

The lateral surface of the head in the salmonines is less fully invested in bone than it is in either the coregonines or the thymallines. The bones either have been reduced or have not kept pace with the greater development of the musculature of the head.

Anteriorly the rounded premaxilla covers the dorsolateral surface of the skull. It is well toothed, bearing from 6 to 9 long, curved teeth. It does not quite touch the premaxilla from the opposite side. This separation may be greater in old adults, forming a ventral groove to receive the long, hooked mandible. Posteriorly the premaxilla articulates with the inwardly curved portion of the maxilla and is prevented from touching the palatine at this point. The ascending process of the premaxilla, which lies against the supraethmoid, is somewhat distinctive among the genera of salmonines. It is present in the young of all species, although it is not quite so well developed in *Oncorhynchus*. However, at maturity there are differences. In *Oncorhynchus*, the ascending process has become reduced and almost disappears, whereas in *Salvelinus* it is strong and extends well backward (Pl. 9, B). In *Salmo gairdneri*, *S. trutta*, *Hucho hucho*, and *Brachymystax lenok*, the ascending process is present (Pl. 13, C, H, and D), but it is not so pronounced as in *Salvelinus*.

The maxilla is a long, narrow, slightly curved bone which, except for size, is quite similar to that of the grayling. Teeth are well developed on the maxilla (except on anadromous species when in the sea) and extend along three-fourths the length of the bone (Pl. 10, C). In the migratory salmonines which spend part of their life in the sea, the teeth are short, curved and attached only to the skin. The anterior and posterior one-eighth of the maxilla is devoid of teeth. In juveniles (total length about 65 mm) teeth are fewer in number, but they are well developed in *Salvelinus namaycush* and are smaller and more numerous in *Oncorhynchus*, than in other species studied. In all salmonines, the maxillary teeth are always smaller than the premaxillary teeth (Pl. 13, C, D, and H).

The supramaxilla is a narrow splint-like bone slightly wider posteriorly and coming to a point anteriorly, similar to that in the grayling (Pl. 13, C, D, and H).

The circumorbitals usually number 7 bones (Pl. 10, C) though there are 8 in the grayling and whitefishes. The first 2 are the supraorbitals which do not bear a lateral-line canal.

The lachrymal, the 3rd bone in the circumorbital series, curves upward in front to meet the 2nd supraorbital. The infraorbital canal terminates in the lachrymal, which displays distinctive features. In *Salvelinus namaycush* and *Brachymystax lenok*, it is somewhat rounded in front, as in *Stenodus* but in *Oncorhynchus*, *Salmo gairdneri*, *S. trutta*, and *Hucho hucho* it is more rectangular, similar to that in *Thymallus*.

Behind the infraorbital, 3 (occasionally 4) postorbitals are found in the salmonines. The 2nd postorbital is the longest, whereas in the grayling and whitefishes (except *Stenodus*) it is the 1st postorbital that is the longest. A further distinction from the former 2 groups is noted in the direct articulation of the 3rd (uppermost) postorbital with the frontal and pterotic. The infraorbital canal is transmitted directly to the lateral canal in the pterotic. No dermosphenotic is present in salmonines. Except in *Oncorhynchus*, the postorbital bones fail by a wide space to reach the preopercle; often they extend less than half way across the cheek (Pl. 10, C). The 2nd postorbital of all adult Pacific salmons (*Oncorhynchus*) extends backward and touches the preopercle, as it does in *Thymallus*, *Coregonus* and *Prosopium* but not in *Stenodus*. This backward growth commences early and is already observed to be twice as broad as it is in lake trout specimens of 65 mm total length.

The dentary is a strong, well-toothed bone comprising the greater part of the lower jaw (Pl. 10, C). The number of teeth is variable but at least 10 are present, and in non-anadromous forms these are fused to the dentary. The teeth are fused also in juveniles of *Oncorhynchus* before they migrate to the sea. In specimens of *Oncorhynchus nerka* and *O. keta* obtained from the Pacific Ocean, the small teeth are loosely embedded in the skin. A similar condition exists in *Salmo salar* (Tchernavin, 1938a). As in the grayling, the lower arm of the dentary is the longer, but it does not extend far enough caudad to touch the retroarticular as it does in the coregonines.

As in other salmonids, the triangular-shaped angular bone fits into the curved mesial surface of the dentary. The inner surface of the angular has become ossified around the posterior end of Meckel's cartilage, which then extends forward to fit into the anteromesial groove in the dentary. The retroarticular is located at the posteroventral corner of the angular. Also present is a small coronomeckelian, located on the mesial surface of the angular and lying over Meckel's cartilage. Except for the contact of dentary and retroarticular in the Coregoninae, these 3 bones have little taxonomic significance among the salmonids.

The preopercle, in contrast with its prominently arched form in the grayling and whitefishes is only gently curved. The horizontal arm is only about one-fourth to one-third the length of the vertical arm (Pl. 10, C). It is attached by tough fascia to the corner of the lower jaw and quadrate. The preopercle is rather uniform among the Salmoninae. In the Salmonidae, the suprapreopercle is peculiar to the Salmoninae (Pl. 10, C). It is a small tubular bone lying between the dorsal tip of the preopercle and the pterotic. The 3 remaining opercular bones have little taxonomic significance at the generic level among the salmonids.

The branchiostegal rays in the Salmoninae are rather large fan-shaped bones covering much of the ventral surface of the head. They are generally more numerous in the salmons and trouts than in the grayling and whitefishes. The minimum number 8, reported in *Salmo gairdneri* (Needham and Gard, 1959), is the same as that found in many species of *Coregonus* and *Prosopium*. The 11 branchiostegal rays found in *Salmo ohridanus*, *Salvelinus fontinalis*, and *Hucho perryi* is equal to the maximum for *Stenodus leucichthys*, but as many as 15 are present in *Salvelinus malma*. From 10 to 19 were counted by Clemens (1935: 105) in various species of *Oncorhynchus*. The number of branchiostegal rays is of limited taxonomic utility in the Salmoninae because of the variation and overlap among species. The posterior 2 or 3 rays are attached to the epihyal, the remainder to the ceratohyal.

Ventral Bones of Cranium

The vomer has received considerable attention from ichthyologists because of its use as a systematic character to separate *Salmo* from *Salvelinus* and, further, to separate the lake trout from other chars. The vomer in the salmonines is much larger than in either of the other subfamilies. In *Oncorhynchus* and *Salmo*, it is a narrow flat plate armed with teeth along its entire length. The teeth are fused to the vomer in the juveniles but are small and deciduous when they migrate to the sea. In contrast, the vomer of the char (*Salvelinus*) is shaped like an inverted boat hull, with a dorsal keel and a ventral crest. Most of the teeth are borne on the anterior enlarged head, with few at most, on the crest. The tapering shaft is toothless. The toothed crest in the lake trout has been used to separate this species as a separate genus (*Cristivomer*), but Kendall (1914: 10; 1919: 70–80), Regan (1914: 408) and more recently Morton and Miller (1954) have shown that intermediate conditions exist in the Arctic chars. Nomura (1953: 263; 1954: 237) has used the presence and relationships of the teeth on the vomer and palatines as a means of separating 3 genera of salmonids (*Oncorhynchus*, *Salmo*, and *Salvelinus*). In *Oncorhynchus*, the teeth on the roof of the mouth are arranged in 2 lateral bands on the palatine bones, a toothless gap, and a straight band on the shaft of the vomer (Fig. 1, F). In *Salmo*, the shaft of the vomer is toothed and there is little or no gap between the palatine and vomerine teeth (Fig. 1, E). The toothed outline thus formed is T-shaped. In *Salvelinus*, teeth are present on the palatines but with a short gap between them (Fig. 1, D). *Brachymystax* and *Hucho* are alike in that the shaft of the vomer is toothless and the palatine teeth are continuous with those on the vomer, thus forming a semicircular band of teeth around the anterior margin of the palate (Fig. 1, B and C).

The digitate anterior part of the parasphenoid is overlapped by the vomer in all species of Salmoninae studied. The anterior end of the parasphenoid is rather flat, but when it reaches the otic region, it bends upward to form the floor and most of the sidewalls of the posterior myodome.

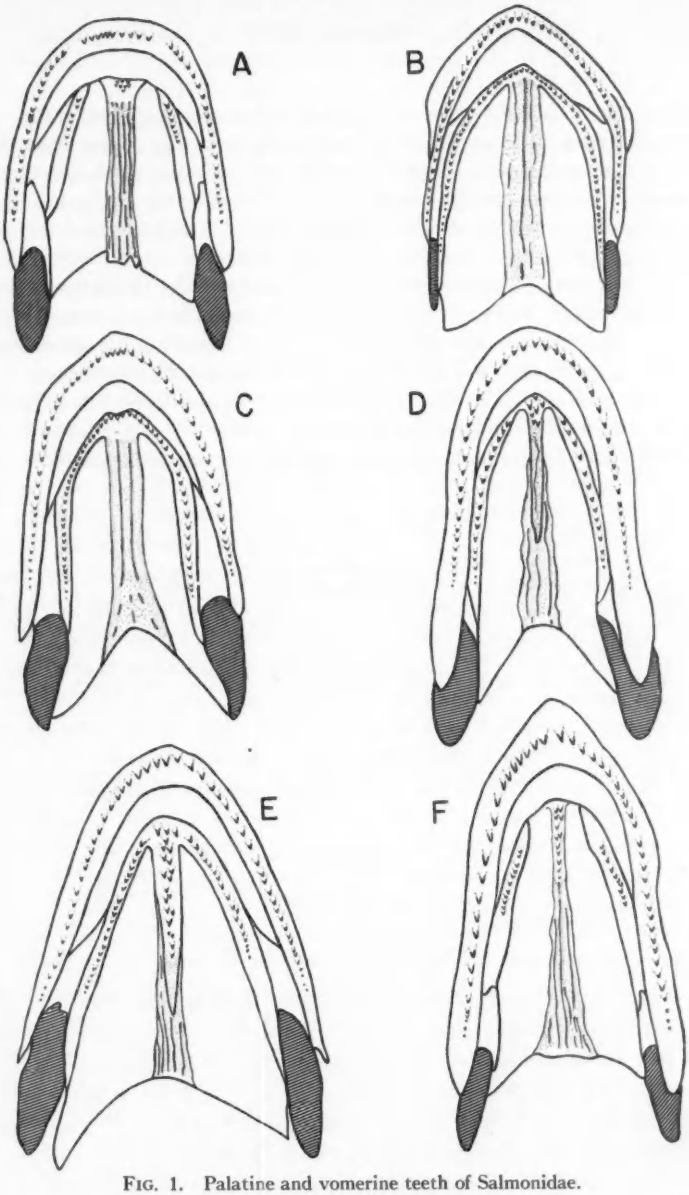

FIG. 1. Palatine and vomerine teeth of Salmonidae.
A. *Thymallus arcticus*, UMMZ 172465, about 0.9×
B. *Brachymystax lenok*, UMMZ 172490, about 1.7×
C. *Hucho perryi*, UMMZ 172493, about 1.7×
D. *Salvelinus fontinalis*, UMMZ 172462, about 0.7×
E. *Salmo trutta*, UMMZ 172470, about 0.65×
F. *Oncorhynchus nerka*, UMMZ 167467, about 0.7×

Visceral Arches

Palatoquadrate Arch

The palatine is well toothed in all the salmonines, although the teeth are small and free from the bone in species of *Oncorhynchus* and *Salmo* when they enter the sea. In all genera except *Oncorhynchus* the palatine teeth are more or less continuous with those on the vomer (Fig. 1). Anteriorly the palatine is larger and bears two well-developed cartilaginous knobs. The first articulates with the ethmoid cartilage in front and the second behind the prefrontal bone. Posteriorly the palatine narrows to a thin splint and is overlapped by the ectopterygoid.

The distinctive difference in the salmonine quadrate lies in its position rather than in its size or shape. In the graylings and whitefishes, its articulation with the angular is below the eye, whereas in trouts (except *Brachymystax*) it lies well back of the orbit (Pl. 10, C). In *Brachymystax* the quadrate articulation is located in a line with the posterior border of the eye. Its relationship to the ectopterygoid, mesopterygoid, symplectic, preopercle and palatoquadrate cartilage is similar.

Hyoid Arch

The hyomandibulars, symplectics, interhyals, epihyals, ceratohyals, and hypohyals in the Salmoninae differ little from those of the grayling and whitefishes.

The basihyal is cartilaginous, overlaid with a rather long, well-ossified lingual plate (Pl. 6, B). The lingual plate of the salmonines bears from 8 to 12 strong teeth arranged in a series around the outer 3 edges of the bone, although in *Hucho perryi* a few small teeth were observed in the centre of the bone as well. The posterior edge of the lingual plate overlaps the first basibranchial. The well-toothed condition is reminiscent of *Coregonus artedii*, *Prosopium coulteri*, and *Stenodus leucichthys*, but the dental arrangement is different in that teeth are scattered over the bone in the three species of whitefishes. The elongate shape is somewhat like that in *Stenodus* and *C. artedii*, but it is not at all like the spatulate lingual plate in *Thymallus arcticus* (Pl. 6).

Branchial Arches

The basic pattern of the branchial skeleton is similar throughout the salmonid fishes. All, including the trouts, have 3 pairs of ossified pharyngobranchials, the first pair being attached to the parasphenoid. A small pharyngeal plate is found on the 3rd pharyngobranchial (Pl. 6, B). The plate is small and poorly developed with only 1, 2, or 3 teeth present in *Salmo salar*, *S. trutta*, and *Brachymystax lenok*; it is like *Prosopium cylindraceum*, *Coregonus artedii*, and *C. clupeaformis*. The pharyngeal plate is better developed in the other salmonines studied, especially *Salvelinus fontinalis*, *S. namaycush*, *Hucho hucho*, and *H. perryi*. The last 4 species are comparable to *Thymallus articus* but the teeth are not as numerous as in *Stenodus leucichthys*.

There are 4 pairs of epibranchials, the 4th being atypical and bearing a pharyngeal plate as in the grayling and whitefishes (Pl. 6, B). Five pairs of ceratobranchials are present, the 5th being broad, anteriorly, and covered with the 3rd and largest pharyngeal plate (Pl. 6, B). Three pairs of hypobranchials are present and are similar in shape and mode of articulation to the same bones in the grayling. Short blunt gill rakers are present on the anterior faces of all 5 arches. When present on the posterior surfaces of the arches, the gill rakers are much smaller and are irregular in occurrence. Tchernavin (1938a) mentioned their presence on *Salmo salar* but said they were lacking in *Oncorhynchus*. The presence of posterior gill rakers was verified on some specimens of *Oncorhynchus nerka*, *Salmo gairdneri*, *S. clarki*, *S. ohridanus*, *Salvelinus fontinalis*, *S. namaycush*, *Hucho hucho*, *H. perryi*, and *Brachymystax lenok*.

There is a series of 4 basibranchial bones which lie on the floor of the pharynx. In all salmonines 1 or 2 dermal basibranchial plates cover the area between the middle of the 2nd basibranchial and the middle of the 4th basibranchial (Pl. 6, B). They are fused to the 3rd basibranchial and may or may not bear teeth. The teeth are well developed in *Hucho perryi*, *Salmo clarki*, and *Salvelinus namaycush*, and are reported to be present in most other species of *Salvelinus*. In *Salvelinus fontinalis* the teeth are feebly present or are absent (Pl. 6, B), but they are lacking in all other salmonine species studied (including *Salmo gairdneri*, *S. salar*, *S. ohridanus*. *Hucho hucho*, *Oncorhynchus tshawytscha*, *O. nerka*, and *Brachymystax lenok*). The basibranchial plate corresponds to that found in the genus *Prosopium*. The dentigerous condition, when present, is not like that found in *Coregonus artedii* and *Stenodus leucichthys*, in which the teeth are implanted in skin.

Urohyal

A urohyal is present in all trouts, its shape being similar to that in the related forms studied.

Axial Skeleton

Vertebral Column

The number of vertebrae in the salmonines ranges from 55 in *Salmo trutta* (Tåning, 1952), *S. gairdneri* (Needham and Gard, 1959), and *Salvelinus fontinalis*, to 72 in *Oncorhynchus tshawytscha* (Foerster and Pritchard, 1935). Tåning (1952: 184) has cited counts of 53 and 54 in *Salmo trutta* but he suggested the possibility that they stem from vertebral fusions. The maximum number of vertebrae (72) is higher than in any other salmonid.

The shape and size range of the vertebrae are the same as in the grayling. Neural arches and spines are borne on the centra. The arches lie in circular pits, and those anterior of the dorsal fin are not fused to the centra. The neural spines anteriorly of the dorsal fin are bifurcated, while those behind it are simple and slope caudally. The last three or four are somewhat expanded. Epineurals are present on the first 30 to 36 vertebrae and slant caudally from near the base of the neural arches.

Ventrally the centra bear rounded pits which receive the parapophyses supporting the ribs. The parapophyses of about the first 30 vertebrae are not fused to the centra. Posteriorly, they lie progressively farther forward on the centra and are fused with them. The parapophyses bear short pre- and post-zygapophyses that do not articulate between centra. Long, 2-headed pleural ribs articulate with the parapophyses. The last 6 or 8 ribs have rounded heads and are loosely attached to the longer parapophyses. Epipleurals are typically lacking among the salmonines. Among the species studied, they were found only in *Salvelinus fontinalis*, and in this species they are subject to individual variation, being developed in only 5 of 14 specimens examined. In these 5 the ribs were considerably expanded dorsally, the expanded part forming a free spine that is dichotomous on many ribs. From 15 to 23 pairs of ribs bear epipleurals.

The parapophyses of the 5 to 7 precaudal vertebrae are elongate and bridged, forming haemal arches and a haemal canal. The caudal vertebrae are characterized by the presence of caudally-directed haemal spines; the last 3 or 4 (excluding the 7 hypurals) of which are somewhat expanded. The number of caudal vertebrae is positively correlated with the total number of vertebrae present. Thus, in a specimen of *Salvelinus fontinalis* having 56 vertebrae, 22 are caudal, while in *Oncorhynchus tshawytscha* with 69 vertebrae, 30 may be caudal vertebrae.

The basic structure of the caudal fin is fairly constant among the salmonines. There is little variation in the number of principal caudal rays, which typically number 19, occasionally 18 or 20. Three upturned terminal vertebrae, 7 hypurals, and 3 pairs of uroneurals are present as in the grayling and whitefishes. The dorsal crest of the anterior uroneural is more strongly developed in *Salvelinus fontinalis*, *Salmo gairdneri*, and *Hucho perryi* (Pl. 14, A and C, Pl. 15, C) than in *Oncorhynchus*. Two epurals usually are present in *Salvelinus fontinalis*, *S. namaycush*, *Salmo salar*, *S. trutta* (Pl. 14, A, B, E, and F), and occasionally in *Oncorhynchus keta*, *O. nerka*, and *O. tshawytscha*. This seems to be a variable character, however, because sometimes both the arch and the spine belonging to the 3rd terminal centrum may be present, the spine alone may be absent, or both may be absent. *Salmo gairdneri* regularly has 3 epurals (Pl. 14, C). Three epurals occasionally are present in *Salmo trutta*, (Pl. 14, D), *Oncorhynchus nerka*, *O. tshawytscha*, *O. kisutch*, and *Hucho perryi* (Pl. 15, A and C). Apparently in these species either the 3rd terminal neural arch has been lost or it has become fused with the anterior uroneural, with the neural spine remaining as an epural. A cartilaginous urostyle curves dorsally and terminates in a blunt tip between the roots of the caudal fin rays.

Median Fins

The dorsal fin of the trouts is similar to that of the grayling, except that it has fewer rays. None of the Salmonines counted had more than 16 dorsal rays, which is one less than the minimum recorded for a grayling. The dorsal ray count in the trouts is of little value as a taxonomic character, because it may vary from a low of 11 in *Salvelinus fontinalis* to a high of 16 in *Oncorhynchus tshawytscha*.

The variability in each species is about 4 rays; for example, the range for *Salvelinus fontinalis* is 11 to 14. The number of rays corresponds closely with that in the coregonines. As in the grayling and whitefishes, the dorsal rays are supported by a series of 3 pterygiophores. Fourteen to 20 interneurals lie between the atlas and the dorsal fin and project ventrad between the bifid neural spines.

Except for location, the characteristics of the anal fin are the same as the dorsal fin. Although it does not appear to be a particularly significant character, the higher number of anal rays (16 to 20 recorded for the Pacific salmon) has been used as one means of separating the genus *Oncorhynchus* from the rest of the trouts. This figure is higher than those recorded by Foerster and Pritchard (1935: 110) who did not count those rays which are less than one-half as long as the longest ray. However, it is impossible to separate *Salmo* from *Oncorhynchus* on this basis alone as the numbers overlap to some extent, and vary from 11 to 15 anal rays (the latter observed in one specimen of *Salmo gairdneri*). Although no overlap occurs between the North American species of *Oncorhynchus* and *Salmo*, an intermediate condition exists in the Asiatic *Oncorhynchus masou*, which has from 13 to 15 anal rays. The same observation was made by Regan (1914: 407). With the exception of *Oncorhynchus*, the number of anal rays in the salmonines overlaps both the thymallines and coregonines. The long antero-dorsally directed pterygiophores are equal to, or 1 or 2 less than, the number of anal rays present.

Appendicular Skeleton

Pectoral Girdle

There is little to add in a description of the pectoral girdle of the salmonines that has not already been mentioned for the coregonines and thymallines. The same bones are present, and in the same locations. The scapular foramen is entirely within the scapula. A mesacoracoid, and three postcleithra are present, with the 3rd being long and pointed, as in *Thymallus* and *Coregonus*. The 1st postcleithrum usually overlaps the 2nd and if not, there is only a short gap between them. Four actinosts are commonly present, occasionally 5, and 6 were found in a specimen of *Salmo gairdneri* (Norden, 1959).

The number of rays in the pectoral fin varies from 12 in *Salmo trutta* and *Salvelinus fontinalis* to 17 in *Oncorhynchus nerka* and *O. keta*. In general, the fin-ray count for *Oncorhynchus* is slightly higher than for trouts, with a range of 14 to 17 rays.

Pelvic Girdle

The pelvic girdle of the trouts is not different from other salmonid fishes, consisting of a pair of L-shaped basipterygia which meet at two points in the midline. A curved pterygiophore, an axillary process, and 8 to 11 fin rays are present. A minimum of 8 pelvic rays is recorded for *Salvelinus fontinalis*, and a maximum of 11 in *Salmo gairdneri*, *Oncorhynchus nerka*, and *O. tshawytscha*.

THE CAUDAL SKELETON

The 3 upturned vertebrae in the caudal fin provide a major characteristic of the Salmonidae. There is no basic morphologic difference in the cauda skeleton among the Salmoninae, Coregoninae, and Thymallinae (Gosline, 1960). The 7 hypurals, 3 pairs of uroneurals and cartilaginous urostyle are common to the 3 groups. The greatest variation is noted in the anterior (largest) pair of uroneurals and the epurals. The Coregoninae and Thymallinae are relatively stable in these 2 characteristics, both subfamilies have 2 epurals and the dorsal arm of the first uroneural is only slightly enlarged (Pl. 14, G and H, Pl. 15, B). The Salmoninae are more variable, and may have 2 or 3 epurals and an enlarged dorsal crest on the first uroneural (Pl. 14, Pl. 15, A and C).

From study of developmental stages at the onset of ossification to adulthood, it appears that paired uroneurals 2 and 3 are remnants of the neural arches which belong to the urostyle, whereas the 1st pair of uroneurals is developed from neural arches derived from the last 2 or 3 upturned vertebrae. The epurals represent the neural spines belonging to these arches. It appears further that there is progressive reduction in parts and a change in their relation to the centra. Thus, if the primitive condition consists of 3 distinct neural arches with spines, the following variations have occurred. (1) The last 2 neural arches have fused to form the 1st pair of uroneurals and the neural spines have remained separate as 2 epurals. A 3rd neural arch and spine remain but they are separate from the 3rd terminal centrum (Pl. 14, A). Specimens of this type have been found in *Salvelinus fontinalis*, *S. namaycush*, and *Salmo trutta*. (2) The preceding situation maintains, but the neural spine from the 3rd terminal vertebra is lost and the arch remains separate (Pl. 14, B). This type was noted in specimens of *Salvelinus fontinalis* and *S. namaycush*. Specimens falling into these 2 categories each have 2 epurals. (3) The first pair of uroneurals may be derived from the last 3 neural arches, but the 3 spines remain and have become separated from it as epurals (Pl. 14, C and D). Individuals of this type have been found in *Oncorhynchus gorbuscha*, *O. kisutch*, *O. nerka*, *O. tshawytscha*, *Salmo gairdneri*, and *S. trutta*. Vladykov (1954: 914) mentioned the 3 epurals that are present in *Salmo gairdneri* and the whitefishes. In this type, the arch and spine belonging to the 4th terminal centrum is complete but free from it. (4) The first uroneural is derived from the last 3 neural arches, but a spine has been lost and there are only 2 epurals. However, the fourth terminal arch and spine are complete, but separate from the centrum (Pl. 14, E and F). Individuals of this type were found in *Oncorhynchus keta*, *O. nerka*, *O. tshawytscha*, *Salvelinus namaycush*, *Salmo salar*, and *S. trutta*. (5) In some species, the spine of the 4th vertebra is separated from its arch and is located farther backward, forming what appears to be a 3rd epural. However, it obviously belongs to the 4th vertebra. Therefore, the derivation of the 1st uroneurals and the 2 epurals is believed to be the same as in type 4 (Pl. 14, G and H; Pl. 15, B). This has been observed in specimens of *Coregonus artedii*, *C. clupeaformis*, *Prosopium coulteri*, *P. cylindraceum*, *Stenodus leucichthys*, and *Thymallus arcticus* (possibly *Oncorhynchus tshawytscha*) (Pl. 15, A).

(6) The spine belonging to the 4th terminal vertebra has either disappeared or has moved backward and lies so close to the 2 epurals that it cannot be distinguished from them. The 1st uroneural is derived from the last 3 arches, 3 epurals are present, and in some cases the arch belonging to the 4th terminal centrum is in the process of disappearing (Pl. 15, A and C). This type was observed in *Oncorhynchus tshawytscha*, *Hucho perryi*, and *Brachymystax lenok*.

It can be readily seen that considerable variation exists in the caudal supporting skeleton of the salmonid fishes. In the thymallines and coregonines the size and shape of the 1st uroneural, its relation to the epurals, and the modification of the 4th terminal neural arch and spine appear fairly constant, and these structures are quite similar. It is in the salmonines that most variations occur. Thus, in this particular character, the graylings appear to be closer to the whitefishes. However, too much significance should not be attached to the instability of the caudal skeleton in the trouts.

EXTERNAL ANATOMY

Externally the graylings, trouts and whitefishes have much in common which emphasizes their close mutual affinities. All are soft-rayed fishes, having small to moderate-sized cycloid scales, an adipose fin, scaleless head, abdominal pelvic fins, and an axillary process or scute at the axil of the pelvic fin. Although these characters are not unique to this group, taken in combination they are useful in separating salmonids from other groups of fishes.

The graylings, trout, and whitefishes have certain distinguishing features which make it possible to separate the 3 groups. The enlarged dorsal fin, with 17 to 24 rays, sets the graylings apart from the coregonines and salmonines. The smaller scales (usually more than 100 along the lateral line) and the large, well-toothed jaws are distinctive characters of the trouts. The usually silvery colour, small, weak teeth, and usually larger scales characterize the whitefishes.

External characters possessed in common by the graylings and trouts are the toothed maxilla and the similar colour pattern of a bluish- or greenish-gray background mottled with circular spots, regularly found on most adult trout and grayling.

Distinctive features shared by graylings and whitefishes include the relatively deeply forked caudal fin, small mouth, and large scales. The scales in the lateral line of the graylings vary from 72 to 110 (Svetovidov, 1936). For the whitefishes the range is from 54 (*Coregonus tugun*, Berg, 1948 and *Prosopium coulteri*, Eschmeyer and Bailey, 1955) to 120 (*Stenodus leucichthys*, Berg, 1948).

A study of the scales of *Thymallus arcticus* reveals a closer alliance with the coregonines than with the trouts. This is contrary to the view held by Kendall (1935: 8) that the scales of *Thymallus* are more trout-like. Although Lagler (1947) pointed out that scales are of only limited use as taxonomic characters, the salmonid scale may in general be considered archaic. Lagler regarded closely set, regular circuli and the lack of radii as primitive. Measured by these criteria the trouts are most primitive, and *Stenodus* has the most highly specialized scales,

with secondary radii best developed on the posterior (exposed) field. The condition in *Stenodus* is approached by those in *Coregonus clupeaformis*, *C. artedii*, and *Prosopium cylindraceum*. Occasionally a few short secondary radii are present on the posterior field in *Thymallus arcticus*. The shape of the grayling scale is distinctive, especially the embedded portion, which has a wavy margin with 4 to 6 indentations. The closest approach to this condition is found in the coregonines, which have 2 indentations. The embedded field of the trout scale is round.

Sexual dimorphism is present to some extent in all salmonids. It is least well developed in the coregonines, which have pearl organs. These are said by Koelz (1929: 318) to be present on the head and sides of the body in both sexes in *Coregonus clupeaformis*. In *Prosopium cylindraceum*, according to Koelz, they are developed in both males and females but only on the body. In the Great Lakes ciscoes, pearl organs are well developed only in males and are of uniform thickness over the head and sides of the body. Pearl organs have also been observed on the male *Salvelinus namaycush* (Vladykov, 1954.) The enlarged hook on the lower jaw of male salmonines is a sex-influenced character. In the grayling, the dorsal fin rays of the male elongate so that they extend up to or slightly beyond the adipose fin. In the female, the dorsal rays (when depressed) fail to reach the adipose fin.

MUSCULATURE

A comparative study of the muscles was made on 3 species, *Thymallus arcticus*, *Coregonus artedii*, and *Salvelinus namaycush*, representing the 3 subfamilies. Papers on the musculature of the chinook or king salmon, *Oncorhynchus tshawytscha* (Greene and Greene, 1913) and the Atlantic salmon, *Salmo salar* (Tchernavin, 1953), were followed and the muscles described were found in the 3 species. No significant differences in musculature were observed; that is, no loss or change in position of a muscle was noted. This is not unexpected since few bones are absent from any of the species. Those that are absent (i.e., orbitosphenoid, hypethmoid, suprapreopercle, dermosphenotic) are not important to the origin or insertion of muscles. The greatest variation observed was in size, particularly of the jaw muscles. This relates to feeding habits for most of the salmonines, with large mouths and strong jaws, are piscivorous. Thus, the *adductor mandibularis* is large in *Salvelinus namaycush*, intermediate in size in *Thymallus arcticus*, and small in *Coregonus artedii*. Bones which provide attachment for muscles are influenced by their size. For example, the sphenotic bone in *S. namaycush* is large and projects laterally, affording origin for the well-developed *levator arcus palatini* muscle, which elevates the palate. The hyomandibular is also massive in the adult lake trout in which it forms part of the origin of the *adductor mandibularis* muscle and the insertion of the *levator* and *adductor arcus palatini* muscles. The latter muscles originate in part on the orbitosphenoid, pterosphenoid, sphenotic, and pterotic bones in *Salvelinus*, but in *Thymallus*, which does not have an orbitosphenoid, the origin is on the pterosphenoid.

INTERNAL ORGANS

The visceral organs are structurally similar among all the salmonid fishes studied. The gullet bears longitudinal ridges on its inner surface, which continue into the U-shaped stomach. In specimens gorged with food the ridges disappear. A U-shaped stomach appears to be characteristic of the salmonid fishes.

In the grayling, the spleen is usually elongate and attached to the apex of the stomach by peritoneum. In the salmonines, the spleen is more or less triangular or heart-shaped. Little significance can be attached to this difference because much variation exists between the ribbon-shaped spleen of the adult grayling, the small triangular organ in the brook trout, and the intermediate conditions common in the coregonines. The stomach is separated from the intestine by a pyloric sphincter. The anterior end of the intestine is beset with numerous blind tubes, pyloric caeca, which are present in all salmonid fishes. The number of pyloric caeca varies widely, from 11 to over 200. Great diversity in number is noted in forms which are obviously very closely related, a fact which supports the interpretation of Morton and Miller (1954: 122) that the character should be accorded only specific significance in this group. The pyloric caeca of 8 adult grayling from Montana yielded the following counts: 17 (1), 18 (1), 19 (1), 20 (2), 21 (1), 22 (2). These counts are close to those recorded by Eschmeyer and Bailey (1955: 172) for *Prosopium coulteri*, which has a range of 15 to 23 caeca. Svetovidov (1936) reported from 11 to 25 caeca in the Eurasian graylings. Among salmonines, DeLacy and Morton (1943: 90) cited a low of 21 in *Salvelinus malma*, and Vladykov (1954: 913) gave 20 as the lowest count in *Salvelinus alpinus*. The lower part of the intestine is encircled with annuli which become more conspicuous near the anus. This increased absorptive area is equally well developed in all three groups. A bilobed liver and gall bladder also are present. The bile duct enters the duodenal part of the intestine a short distance below the stomach. The large, single-lobed swim bladder connects to the gullet just above its entrance to the stomach.

A pair of pseudobranchs are present in all salmonid fishes. They consist of a few gill filaments lying over the anterior edge of the hyomandibular and the dorsal margin of the metapterygoid bones.

REPRODUCTION AND LARVAL STAGES

The reproductive organs of the three subfamilies are similar, with no differences in shape or location of the gonads. The testis is a long (well over half the length of the intestine), rather flat organ commencing at the anterior end of the stomach and extending much of the length of the peritoneal cavity. The sperm duct, located on the mesial surface of the testis, continues beyond the posterior tip of the testis to the urogenital opening. The pair of sperm ducts join near their external aperture.

The ovaries are of much the same shape as the testis in immature specimens, but in mature spawning females they become turgid with eggs and fill much of the

body cavity. The eggs do not normally break out into the abdominal cavity but are contained in oviducal folds of peritoneum which become narrow and tubular posteriorly just before they pass to the exterior.

The chief apparent difference in the eggs of the trouts, whitefishes, and graylings is in size. The average diameter of the unfertilized grayling egg is about 2.5 mm. This is about the size of the egg reported for the coregonines. That of *Coregonus clupeaformis* was given as 3.0 mm by Price (1934: 290), and Fish (1932: 308, 311) reported the average egg diameter of *Coregonus artedii* to be 2.25 mm and of *C. clupeaformis* 2.8 to 3.0 mm. Smith (1956: 125) gave 1.88 mm as the average diameter of *C. artedii* eggs at the time of spawning in Green Bay. Sigler (1951: 14) gave the egg size of *Prosopium williamsoni* as varying between 1.94 and 2.12 mm and Brown (1952: 110) gave 3.7 as the average diameter of water-hardened eggs for that species. The eggs of the salmonines are somewhat larger. Brown and Kamp (1942: 199) gave the average measurement for *Salmo trutta* as 4.94 mm. Vladykov (1954: 906) recorded the average diameters of eyed eggs from *Salvelinus fontinalis* as 4.0 to 4.4 mm, *S. namaycush* as 5.7 to 5.8 mm and *Salmo salar* as 5.4 to 6.8 mm. Tchernavin (1923) described the spawn of *Brachymystax* as fine, but gave no measurements. In general, the salmonine egg is about twice the diameter of the whitefish and grayling egg. This presumably accounts for the absence of a postlarval stage in the salmonines, whereas such a stage is present in the coregonines and thymallines.

Winn and Miller (1954: 276) defined postlarval life as "the period after the adsorption of the yolk to a stage when the fish resembles the juvenile." In the grayling, the transformation from postlarva to juvenile may be recognized by the loss of the continuous fin fold, the development of parr marks and commencement of ossification in the fin rays. This occurs when the young fish have reached a total length of 33 to 40 mm about 64 to 78 days after hatching. At a total length of 15.5 mm and an age of 16 days after hatching, the grayling is in the postlarval stage and the yolk is completely absorbed. At the same length, the lake trout, on the other hand, has a large yolk sac (measuring 7.25 mm in length and 4.5 mm in width). Day-old grayling (total length about 11.0 mm) have a small yolk sac (3.2 by 2.0 mm). Watling and Brown (1955: 93) recorded an average size range of 2.5 to 2.8 mm in the length of the yolk sac on the day of hatching. The yolk sac disappears about 13 days after hatching. Early stages for *Coregonus artedii* and *C. clupeaformis* have been described and figured by Fish (1932: 308–315) which are similar to those of *Thymallus arcticus* of the same age. When young lake trout are about 30 mm in total length the continuous fin fold has disappeared and parr marks have appeared; they then look like juveniles. In grayling of comparable length, the continuous fin fold has disappeared but the adipose fin is long and parr marks have not yet appeared. The grayling, now 52 to 55 days old, are still in the postlarval stage. Seventy-eight days after hatching, the grayling have reached a total length of 40 to 50 mm and are now developed juveniles with parr marks, a long dorsal fin and considerable ossification in the fin rays, vertebrae and some of the skull bones. Lake trout of similar size are in the same stage of ossification.

Parr marks, consisting of black pigment under the skin in a pattern of vertical bars or oval blotches along the side, are a rather common feature among the salmonids. The grayling has an average of 13.4 oval parr marks which are bisected by the lateral line. Parr marks also are present, at least in the young, in the genera *Salmo*, *Salvelinus*, *Brachymystax*, *Hucho*, *Oncorhynchus* (except *O. gorbuscha*, Foerster and Pritchard, 1935) and *Prosopium*. Young of *Prosopium abyssicola* and *P. gemmiferum* were not available for this study. They are absent from *Stenodus* and *Coregonus*.

The development of the young grayling has much in common with that of both the coregonines and the salmonines. The size of the egg and the postlarval stage suggest a closer relationship with the whitefishes, but the possession of parr marks tends to link *Thymallus* with the trouts and *Prosopium*. In the latter character, it is *Stenodus* and *Coregonus* that are set apart, and Walters (1955: 289) used this as one reason for segregating *Prosopium* as a genus distinct from *Coregonus*.

FOSSIL SALMONIDAE

The origin of the suborder Salmonoidei has been variously placed between the Upper Cretaceous and the Lower Eocene. Cockerell (1919) and David (1946a) have described fish scales from the Upper Cretaceous as belonging to or closely related to the family Salmonidae. Cockerell (1919) stated that the scales bear a resemblance to the Thymallidae, but since scales are of questionable taxonomic value, it is well not to attach too much significance to them. A fossil salmonoid fish *Thaumaturus furcatus* (Reuss) has been reviewed by Laube (1900) from the Miocene of Bohemia. From the description and figure of the single caudal vertebra, it seems likely that this fish is allied to the Argentinidae or Osmeridae, although Berg (1940) erected a new family, Thaumaturidae, for this genus. Laube (1901) described as thymallids two fossil species, *Protothymallus lusatus* and *P. princeps*, from the Miocene of Bohemia. The figures give no basis for believing that they are more closely related to *Thymallus* than to any other salmonid. They do, however, show 3 upturned caudal vetrebrae.

The few papers published on fossil salmonoids indicate that the Argentinidae and Osmeridae were separated from the Salmonidae at the beginning of the Miocene. Eastman (1917) reported an undetermined fossil related to *Osmerus* from the Oligocene or Lower Miocene of Montana, David (1943) described a form belonging to the family Bathylagidae from the Upper Miocene of California, and Weiler (1943) described 3 species of *Argentina* from fossil otoliths found in the Upper Tertiary of Romania.

Fossil remains of the salmonids are scanty and, partly for this reason, the recent genera and species are believed to be of rather modern origin, perhaps Pliocene or early Pleistocene. One reason for the scarcity of fossil material is the lack of interest by paleontologists in the ichthyofauna of these last two epochs. Perhaps the best known salmonid fossil is of *Rhabdofario*, described by Cope (1870) from the Pleistocene of Idaho and believed by Cope to be closely allied to

Salmo. Another possible explanation for the paucity of fossil salmonids rests on an ecological preference for habitats that are not conducive to easy fossilization.

Just where the separation of the coregonines, thymallines, and salmonines occurred poses a problem. The only available fossil material is from 2 or 3 scales obtained from the Upper Eocene or early Oligocene of California, which David (1946a) used to describe two new fossil species assigned to the Coregonidae. One of the scales shows similarity with the scales of *Stenodus*, the other, with those of *Coregonus nigripinnis*. As previously mentioned, little reliance should be placed on these two species. Good fossil material of the Salmonidae is a prime desideratum in a solution of the evolutionary history of the group.

SYSTEMATIC POSITION OF THE SALMONIDAE

Seven families (Salmonidae, Plecoglossidae, Osmeridae, Argentinidae, Salangidae, Retropinnatidae, and Aplochitonidae) at present are assigned to the suborder Salmonoidei. The osteology and relationships of the Osmeridae, Argentinidae, and Plecoglossidae have been worked out by Chapman (1941a, 1941b, 1942), and I have had study material available for these families (Table III). The Salangidae, Retropinnatidae, and Aplochitonidae were not studied.

In the Argentinidae, such characters as the placement of the paired fins, presence of an adipose fin, orbitosphenoid, basisphenoid, mesocoracoids, 3 posteleithra, epipleural spines, opisthotics, an open posterior myodome, toothed palatine and vomer, toothless maxilla, and the parietals meeting in the midline are found to be common also to some or all representatives of the Salmonidae. The Argentinidae are distinguished from the Salmonidae by the presence of one or two (Gosline, 1960) upturned caudal vertebra, the first uroneural does not extend forward beyond the penultimate centra (Gosline, 1960), edentulous premaxillae, lack of supramaxillae, the strong attachment of the palatine to the ethmoid region, and a swim bladder that lacks a connection with the gut (Cohen, 1958).

Features common to some species of both the Osmeridae and the Salmonidae are the presence of opisthotics, mesocoracoids, epipleurals, a toothed basibranchial plate, a shaftless but toothed vomer, an adipose fin, parietals which may or may not be separated by the supraoccipital, and an open posterior myodome. The Osmeridae are distinct from the Salmonidae because they have toothed mesopterygoids, a single upturned caudal vertebra, proethmoids, and a pouch-like stomach, which in *Osmerus mordax* has from 4 to 6 pyloric caeca.

The Plecoglossidae bear numerous resemblances to at least some of the Salmonidae in that they lack an orbitosphenoid and a basisphenoid, have numerous pyloric caeca, a toothed basibranchial plate, mesocoracoid bones, an adipose fin, and pseudobranchia. The Plecoglossidae are distinct in that they have no postcleithra, no supramaxillae, a single upturned caudal vertebra, toothed mesopterygoid, toothless vomer, and specialized oral organs.

These 3 families are of interest in this study because of the loss or modification of certain characters which appear to be distributed somewhat haphazardly

among the salmonids. For example, the orbitosphenoid is absent in the graylings, osmerids, and *Plecoglossus*, but is present in the trouts, whitefishes, and argentines. The basibranchial plate is present in the osmerids, trouts, *Plecoglossus*, and *Prosopium* but is absent in the argentines, graylings, *Coregonus*, and *Stenodus*. In the family Osmeridae, 3 genera have the parietals meeting in the midline, whereas 3 others have the parietals separated by the supraoccipital, thus paralleling the condition in the Salmonidae. Thus certain characters which seem, at first, to be distinctive for the grayling also appear in related families.

The Salmonidae are most easily separated from the Argentinidae, Osmeridae, and Plecoglossidae by having 3 rather than 1 or 2 upturned caudal vertebrae. In possessing 3 upturned caudal vertebrae, the Salmonidae, show a closer affinity to the basic isospondylous stock such as the Elopidae and Albulidae. *Elops saurus* and *E. affinis* have 4 upturned caudal vertebrae (Pl. 15, D). *Megalops atlantica* Valenciennes also has 4, whereas the adult of *Albula vulpes* (Linnaeus) has 2 upturned centra (Hollister, 1936).

A combination of characters which are peculiar to the trouts, whitefishes, and graylings, suggest that this is a single circumscribed group and that *Thymallus* is as much a part of it as any of the genera described. First, the 3 subfamilies possess a number of primitive characters in common. These include soft fin rays, cycloid scales, an open pneumatic duct, an adipose fin, the maxilla forming part of the margin of the gape, numerous branchiostegal rays, parapophyses not coossified with the centra, oviducts incomplete, and the 3 upturned vertebrae in the caudal skeleton.

Second, certain characters which might be expected to accentuate divergence among groups, tend instead to show relationship. For example, vertebral counts in each of 16 species of salmonid fishes (7 genera) indicate that despite the presence of apparently reliable differences between some species, the variation is gradual and overlapping, rather than abrupt, among species and among genera (Table IV).

The sagitta, the largest of the 3 otoliths, was examined for differences of higher taxonomic significance (Pl. 16). Again the variation is such that the otoliths are of little systematic value.

Svärdson (1945) attempted to use chromosome number in taxonomic studies. He found that in salmonoid fishes the chromosome number varied as follows:

Species	Diploid number of chromosomes
Salmo salar	60
S. trutta	80
Salvelinus alpinus	80
S. fontinalis	84
Coregonus lavaretus	80
C. albula	80
Thymallus thymallus	102
Osmerus eperlanus	58

TABLE IV. Frequency distribution of number of vertebrae in selected species of salmonid fishes.

Species	Locality	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70
COREGONINAE																				
Coregonus artedii	Michigan	..	..	..	..	2	1	3	1	3	..	..	..	..	..	..	..	..	..	..
C. clupeaformis	Wisc., Can., N.W.T.	..	..	..	..	..	..	1	2	3	3	..	1	..	..	..	..	..	..	..
C. hoyi	L. Michigan	..	..	..	..	4	2	2	1	1	..	..	..	..	..	..	..	..	..	..
C. kiyi	L. Michigan	..	..	1	2	3	2	1	1	..	..	..	..	..	..	..	..	..	..	..
Prosopium coulteri	L. Superior	2	4	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
P. cylindraceum	L. Mich.; L. Superior	..	..	..	..	..	..	..	1	2	4	1	1	1	..	..	..	..	..	..
P. gemmiferum	Bear Lake, Utah	..	..	4	2	3	..	1	..	..	..	..	..	..	..	..	..	..	..	..
Stenodus leucichthys	Can., N.W.T.	..	..	..	..	..	..	..	..	..	1	1	..	..	1	3	..	2	..	..
SALMONINAE																				
Oncorhynchus nerka	Alaska; Idaho	..	..	..	..	..	..	..	..	..	..	..	..	1	..	4	2	2	1	..
O. tshawytscha	Wash.; Mich. (hatcheries)	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	4	..	4	1
Salmo gairdneri	Michigan	..	..	..	..	..	..	..	1	..	1	3	2	3	..	..	..	..	..	..
S. salar	Maine	..	..	..	..	..	..	2	4	4	..	..	..	..	..	..	..	..	..	..
S. trutta	Mich., Calif.	..	..	..	..	..	..	2	4	3	1	..	..	..	..	..	..	..	..	..
Salvelinus fontinalis	Michigan	..	..	..	4	2	2	1	1	..	..	..	..	..	..	..	..	..	..	..
S. namaycush	L. Superior	..	..	..	..	..	..	..	..	..	..	2	1	3	4	..	..	..	..	..
THYMALLINAE																				
Thymallus arcticus	Montana	..	..	..	..	..	..	..	3	4	4	..	..	..	..	..	..	..	..	..

Although studies of chromosome counts are inconclusive, the data accumulated to the present indicate that there is much overlap and continuous variation. Thus, the pattern of variation in vertebral count (Table IV), the similarity of the otoliths (Pl. 16), and the chromosomal number (Svärdson, 1945) lend support to the hypothesis that the Salmonidae are composed of 3 interrelated groups.

Third, very few of the characters which appear to have value in tracing the evolutionary history of the group (Table V) seem to be diagnostic of a particular genus or even a subfamily. A study of Table V reveals that 3 characters are more fundamental than the others; the absence of an orbitosphenoid bone, the lack of teeth on the maxilla, and the separation of the parietals by the supraoccipital. All 3 are considered specialized traits which foreshadow characters common to the spiny-rayed fishes. If the absence of an orbitosphenoid is used as the basis for separating the 3 groups, then the Thymallinae stand apart from the Coregoninae and Salmoninae. When the edentulous maxilla is used as the primary character the Coregoninae stand alone while the Thymallinae and Salmoninae are grouped together. The broad separation of the parietals by the supraoccipital is diagnostic of the Salmoninae; the Coregoninae and Thymallinae fall into a single category. Since the subfamilies have much in common and assuming these 3 characters are subequal in value, it seems illogical to choose any one feature as diagnostic at a particular taxonomic level. Thus, the unequal emphasis placed on the absence of the orbitosphenoid (Berg, 1940) resulted in the recognition of the graylings as a family, the other groups as subfamilies of the Salmonidae. For the above reasons the trouts, graylings, and whitefishes are placed in a single family, the Salmonidae.

Although the evidence is meager, certain characteristics of the salmonines indicate that they are nearest to the basic salmonid type. This hypothesis is suggested by the following facts: (1) The jaws and mouth are of the generalized pattern typical of numerous other predaceous fishes. It is unlikely that the large, well toothed maxilla was derived from a small, toothless bone such as that of *Coregonus*. *Stenodus leucichthys* is a large-mouthed predaceous fish in which the maxilla borders the gape, yet that bone remains toothless. If teeth once lost could be regained, it seems that this would have occurred in *Stenodus*. (2) The basibranchial plate is probably an old character which has survived in the evolution of the order. In addition to the Salmoninae and *Prosopium* it is present in the Osmeridae and Plecoglossidae (Chapman, 1941a, 1942) and in the Elopidae, Albulidae, and Clupeidae (Ridewood, 1904a, 1904b). (3) The absence of an orbitosphenoid (as in *Thymallus*) is believed to be a recent specialization (Gregory 1933). This bone is large and well developed in the salmonines, as well as in more primitive teleosts such as the Elopidae, Albulidae, and Amiidae. The absence of a basibranchial plate and an orbitosphenoid in *Thymallus* eliminates the modern grayling from consideration as a possible ancestral type of the family (Fig. 2). The chief feature of the Salmoninae in which the entire group is more specialized than the Thymallinae and the Coregoninae is in the separation of the parietals by the supraoccipital. This character has presumably developed since the segregation of the subfamilies.

TABLE V. Characters of chief taxonomic importance in the Salmonidae.

Character	Thymallinae	Coregoninae	Salmoninae
Orbitosphenoid	Absent	Present, small to large	Present, large
Hypethmoid	Absent	Present	Usually absent, occasionally present in *Salvelinus fontinalis* and in *Salmo trutta*
Basisphenoid	Present	Usually present, sometimes absent in *Coregonus*	Present
Parietal Bones	Meeting along midline	Meeting along midline in *Coregonus* and *Prosopium* narrowly separated in *Stenodus*	Separated by supraoccipital
Basibranchial plate	Absent	Present in *Prosopium*; absent in *Coregonus* and *Stenodus*	Present
Dermosphenotic	Present	Present	Absent
Suprapreopercle	Absent	Absent	Present
Median (third) extrascapular on nape	Present	Absent	Usually absent; occasionally present in *Salvelinus namaycush* and *S. fontinalis*
Postorbitals	In contact with preopercle	In contact with preopercle, except in *Stenodus*	Not in contact with preopercle, except in *Oncorhynchus*
Teeth on maxillae	Present	Absent	Present
Jaw articulation	Below eye or at posterior margin	Below eye	Behind eye; below in *Brachymystax*
Teeth size	Intermediate	Small or absent	Intermediate to large
Number of epurals	Two	Two	Two or three
Epipleurals	Present anteriorly	Absent	Usually absent, occasionally present anteriorly in *Salvelinus fontinalis*
Dorsal fin rays (including anterior rudiments)	17 to 25	10 to 15	11 to 16
Scale size and shape	Moderate; with anterior margin fluted	Moderate; with anterior margin round or wavy	Small; with anterior margin round
Parr marks (in young)	Present	Usually absent; present in some species of *Prosopium*	Usually present; absent in *Oncorhynchus gorbuscha*
Egg size	Small	Small	Usually large; small in *Brachymystax*

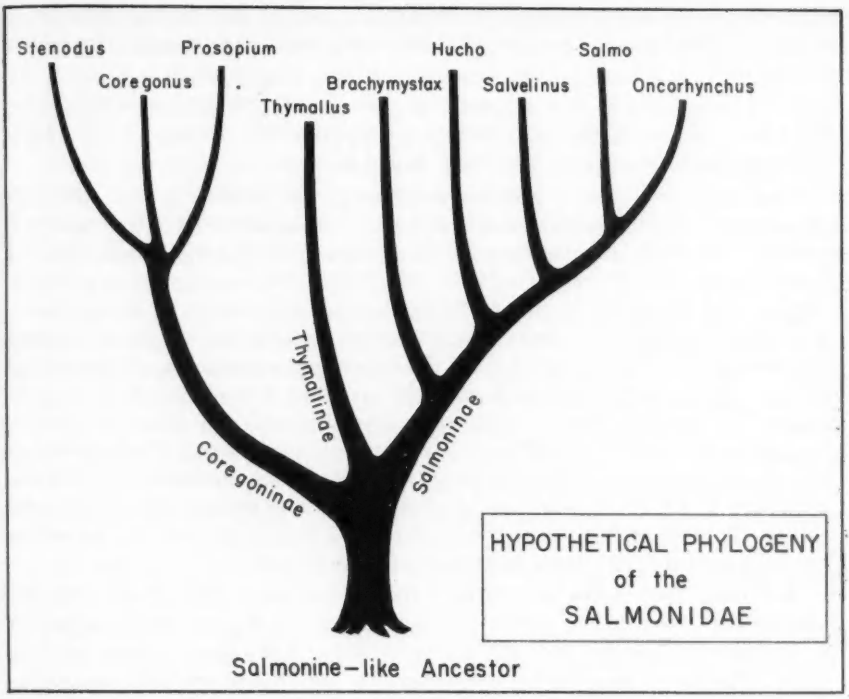

FIG. 2. Hypothetical phylogeny of the Salmonidae.

Among the Salmoninae, *Brachymystax lenok* appears to possess characters closest to the ancestral form of the family. The salmonine features are present but are not strongly developed. For example, *Brachymystax* has a medium-sized mouth, only slightly larger than that in *Thymallus*. Teeth of moderate size are well developed on the maxilla. *Brachymystax* is the only salmonine which produces small ova. One can conceive of an ancestral form like *Brachymystax*, but with the parietals meeting in the midline, evolving into a large-mouthed predaceous *Salmo*, into a weak-jawed insectivorous *Thymallus*, or in still another direction, into a small-mouthed, toothless, plankton-feeding *Coregonus*.

From a *Brachymystax*-like ancestor a salmonine evolutionary trend has probably been marked by a gradual separation of the parietals by the supra-occipital, the fusion of the dermosphenotic with the pterotic or its independent loss, increase in egg size, and the jaws becoming large and more strongly toothed necessitating the displacement of the jaw hinge to a position behind the orbit.

It is possible that *Salmo* represents a form close to the main line of evolution in the salmonines (Regan, 1920; Nall, 1930; Tchernavin, 1937). *Salmo* has the characteristics named in the above paragraph and, in addition, is distinguished

by its colour pattern (dark spots on a light background), the toothed shaft of the vomer, and the T-shaped pattern of teeth on the roof of the mouth (Fig. 1, E).

Hucho appears to be intermediate between *Brachymystax* and *Salmo* (Fig. 2). It differs from *Salmo* in that the shaft of the vomer is not toothed. Therefore, the palatine and vomerine teeth form an oval pattern on the roof of the mouth similar to that of *Brachymystax* (Fig. 1, B and C).

Oncorhynchus is likely a more recent offshoot from *Salmo* (Fig. 2). Although specializations involving habits, physiology, and skeletal characters are well marked in the adult, these are not so pronounced in the young. Thus, some of the characters which Tchernavin (1937: 239, 1938a: 164) used to separate *Oncorhynchus* from *Salmo* are found to be similar in the juveniles of both genera. In juvenile *Oncorhynchus*, dorsal fontanelles are present, the ascending process of the premaxilla is about equally well developed in the two genera, there is little difference in the shape of the supraethmoid, and the arrangement of the teeth is similar. Innovations which characterize *Oncorhynchus* and thus separate it from *Salmo*, at least in the adult, are the backward extension of the postorbitals to touch the preopercle, an anteroventral extension of the opisthotic to touch the prootic, the closure of the dorsal fontanelles, the azygous form of the cartilaginous rostrum, the wide gap between the palatine and vomerine teeth on the palate (Fig. 1, F), and the simultaneous ripening of all germ cells.

Salvelinus may represent a rather early split from the stem form (Fig. 2). It has a distinctive colour pattern and the scales are slightly more specialized than in *Salmo* (Morton and Miller, 1954: 210). Osteological characteristics include the edentulous shaft on the vomer, the length and shape of the supraethmoid (Pl. 12, J), and the elongate ascending process on the premaxilla (Pl. 9, B).

The coregonines are believed to represent an early offshoot of a salmonine-like ancestor (Fig. 2). This separation occurred before the parietals became widely separated by the supraoccipital. It also antedated the loss of the dermosphenotic and (usually) the hypethmoid bones, both of which are well developed in the whitefishes. As indicated on page 747, it does not seem likely that the evolutionary process went the other way (Coregoninae to Salmoninae).

The Coregoninae are of interest because of their adaptive modifications for particular feeding habits. They also afford examples of parallel evolution. If the coregonines evolved from an ancestor similar to *Brachymystax*, they came from an insectivorous or piscivorous type with well-developed jaws. The first step in its evolution was either toward planktonic feeding, presumably involving development of numerous, long gill rakers, or toward bottom (detritus) feeding in which the mouth became small and the gill rakers remained short. In either event maxillary teeth were lost and those on the other jaw bones were reduced in number and strength.

Prosopium may be nearest the ancestral type since it shares two primitive characters with the trouts: parr marks are known to occur in at least some species and a basibranchial plate is present. The evolution of *Coregonus* and *Stenodus*

is marked by the loss of the basibranchial plate and parr marks. *Stenodus leucichthys*, therefore, is a whitefish which has evolved trout-like feeding habits necessitating a large mouth, strong jaws, and teeth. Since large canine teeth were perhaps irrevocably lost the new dentition features numerous, small pointed teeth on the tongue, palate, and in the skin covering the gill arches.

That *Prosopium* could have given rise to a plankton-feeding form with numerous long gill rakers is borne out by *P. gemmiferum*. That this species is a *Prosopium*, likely evolved at a much later date, is indicated by the presence of a basibranchial plate and the similarity of the supraethmoid bone (Pl. 12, C, D, and G).

The "cisco type" (*leucichthys*-group of Gasowska, 1960) has specialized in planktonic feeding and may have given rise to the bottom-feeding forms (*Coregonis clupeaformis* and *C. nasus*), although there is no evidence for this. The reverse evolutionary trend may have occurred with the small-mouthed, bottom-feeding species being ancestral to the planktonic forms, paralleling the evolution of *Prosopium gemmiferum* from a bottom-feeding *Prosopium*. The coregonids exhibit a great deal of plasticity (Smith, 1957) and thus their ancestry is not clear. That *Coregonus clupeaformis* and *C. nasus* are not in the direct line of evolution to *Prosopium* is indicated because they lack a basibranchial plate, have no parr marks, and the supraethmoid is short and triangular rather than elongate and straight (Fl. 12, A, C, and D).

This study reveals that *Stenodus leucichthys* is more closely allied to *Coregonus* than has heretofore been realized (Tchernavin, 1923, placed *Stenodus* in a separate subfamily). However, *Stenodus* Richardson is considered to be a distinct genus (Fig. 2) and differs from *Coregonus* and *Prosopium* in the following features: The orbital ring is closed through enlargement of the first supraorbital and the dermosphenotic; the postorbitals do not touch the preopercle; the mouth is large; the orbitosphenoid is large; the vomer and palatine bear numerous teeth (Pl. 11); the teeth on the dentary and premaxilla are persistent (Pl. 11); the bones are large and heavy; and there are more branchiostegal rays, (9) 10–11 (12) (Fuller, 1955).

The genus *Prosopium* Milner represents an earlier evolutionary line than either *Stenodus* or *Coregonus* and may be distinguished by the following features: A basibranchial plate is present; there is a single narial flap; parr marks are present in the young, of those species for which young are known; the first supraorbital is short; and the supraethmoid is long and narrow (Pl. 12, C, D, and G).

The genus *Coregonus* Linnaeus may be distinguished from both *Stenodus* and *Prosopium* only in that the first supraorbital is intermediate in length. In other characters it agrees with one or the other genus (see above).

Although there are fewer differences between *Prosopium* and *Coregonus* than between either one and *Stenodus*, those that distinguish *Prosopium* from the other groups are judged the more fundamental. As additional evidence on this, *Coregonus* × *Stenodus* hybrids are known (Berg, 1948), but no hybrids involving

Prosopium have been reported. The phyletic separation of *Prosopium* is thus believed to be somewhat older than that between *Coregonus* and *Stenodus* (Fig. 2).

Thymallus may be visualized as descended from a salmonid ancestor (Fig. 2) similar to the recent *Brachymystax* but with the parietals meeting at the midline and with a dermosphenotic bone. The size of the mouth, the location of the jaw hinge, and the dentition on the roof of the mouth (Pl. 13, A and B) are not very different in these genera. The orbitosphenoid is sporadically lacking throughout the suborder Salmonoidei (Plecoglossidae, Osmeridae). The suprapreopercle has been lost also in the Coregoninae, and the dermosphenotic retained in both that subfamily and the Thymallinae. The loss of the epipleurals is not complete in the Salmoninae (e.g., *Salvelinus fontinalis*), and their presence in *Thymallus* may indicate the retention of an old character. The dorsal fin with 17 or more rays, only one more than the maximum in the Salmoninae, is of limited significance and probably is a rather recent acquisition.

I believe the Salmonidae are descended from an ancestral type which had many of the modern salmonine characteristics. However, they have diverged, perhaps during or after the Miocene, into 3 phyletic lines, which are here considered subfamilies. A hypothetical arrangement of the genera of the family Salmonidae is shown in Fig. 2.

SUMMARY

Suborder Salmonoidei (order Clupeiformes), comprising the families Salmonidae, Argentinidae, Osmeridae, Plecoglossidae, Retropinnatidae, Salangidae and Aplochitonidae, has the following characters: Parapophyses not fused to the centra; autogenous haemal processes in the posterior caudal vertebrae; oviducts absent or incomplete; adipose fin usually present; neural and haemal arches and spines of caudal skeleton laterally compressed; and photophores absent.

Family Salmonidae differs from one or more of the other salmonoid families in each of the following: Three upturned caudal vertebrae (unique in Salmonidae); autogenous neural processes in the posterior caudal vertebrae; mesopterygoid toothless (toothed in Osmeridae and Plecoglossidae, absent in Salangidae); 3 postcleithra (absent in Plecoglossidae); mesocoracoid present (absent in Retropinnatidae and Aplochiochitonidae); opisthotic present (absent in Retropinnatidae, Aplochitonidae, and Salangidae); scapular foramen entirely contained within the scapula (not in Plecoglossidae); and pyloric caeca many (11 or more).

The subfamilies and genera of the Salmonidae may be defined as follows: Subfamily Salmoninae consists of salmonid fishes with an orbitosphenoid, suprapreopercle, and basibranchial plate; no dermosphenotic; usually no hypethmoid and epipleurals; not more than 16 dorsal-fin rays; small rounded scales; large-toothed maxilla and premaxilla; usually large ova and no postlarval stage; young usually with parr marks; and parietals separate at the midline.

Five genera are recognized:

Genus *Brachymystax*. Salmonine fishes with relatively small mouth, jaw hinge below posterior margin of eye; no teeth on shaft of vomer; U-shaped band of palatine and vomerine teeth; postorbitals not in contact with preopercle; long supraethmoid with numerous posterior projections; intermediate-sized ascending process of premaxilla; opisthotic not touching prootic; persistent dorsal fontanelles; and small ova.

Genus *Hucho*. Salmonine fishes with large mouth, jaw hinge behind orbit; no teeth on shaft of vomer; U-shaped band of palatine and vomerine teeth; postorbitals not in contact with preopercle; broad supraethmoid, with numerous small posterior projections; intermediate-sized ascending process of premaxilla; opisthotic not touching prootic; persistent dorsal fontanelles; and large ova.

Genus *Salvelinus*. Salmonine fishes with large mouth, jaw hinge well behind orbit; no teeth on shaft of vomer; narrowly separated palatine and vomerine teeth; postorbitals not in contact with preopercle; long supraethmoid with numerous posterior projections; extended and well-developed ascending process of premaxilla; opisthotic not touching prootic; dorsal fontanelles persistent; pattern of light spots on a dark background; and large ova.

Genus *Salmo*. Salmonine fishes with large mouth, jaw hinge behind orbit; teeth on shaft of vomer; narrowly separated palatine and vomerine teeth; postorbitals not in contact with preopercle; supraethmoid notched posteriorly; intermediate-sized ascending process of premaxilla; opisthotic not touching prootic; dorsal fontanelles persistent; pattern of dark spots on a light background; and large ova.

Genus *Oncorhynchus*. Salmonine fishes with large mouth; jaw hinge behind orbit; teeth on shaft of vomer; widely separated palatine and vomerine teeth; postorbitals contacting preopercle; in the adult supraethmoid deeply notched posteriorly; no ascending process of premaxilla; opisthotic touches prootic; in adult no dorsal fontanelles; and large ova.

Subfamily Thymallinae is composed of salmonid fishes with no orbitosphenoid, hypethmoid, suprapreopercle, or basibranchial plate; with epipleurals and dermosphenotic; 17 or more dorsal-fin rays; scales whose embedded margins are indented; toothed maxilla and premaxilla; small ova and a postlarval stage; young with parr marks; and parietals meet at the midline. Subfamily Thymallinae includes a single genus, *Thymallus*.

Subfamily Coregoninae consists of salmonid fishes with an orbitosphenoid, dermosphenotic, and hypethmoid; no epipleurals or suprapreopercle; not more than 15 dorsal-fin rays; large rounded scales; no maxillary teeth; small ova and a postlarval stage; young with or without parr marks; and parietals meet at the midline.

Three genera are recognized, as follows:

Genus *Prosopium*. Light-boned coregonine fishes with an open orbital ring; short first supraorbital; small mouth; a basisphenoid and a basibranchial plate; no or weak teeth; long third postcleithrum; postorbitals in contact with preopercle; elongate supraethmoid; a single nasal flap; and parr marks in known juveniles.

Genus *Coregonus*. Light-boned coregonine fishes having an open orbital ring; intermediate-sized first supraorbital; small mouth; no basibranchial plate; usually a basisphenoid; no or weak teeth; long 3rd postcleithrum; postorbitals in contact with preopercle; short supraethmoid; no parr marks; and 2 nasal flaps.

Genus *Stenodus*. Heavy-boned coregonine fishes with a closed orbital ring; long first supraorbital and dermosphenotic; large mouth; a basisphenoid; no basisbranchial plate; persistent jaw teeth; numerous teeth on vomer and palatine; rounded 3rd postcleithrum; postorbitals not in contact with preopercle; short supraethmoid; and 2 nasal flaps.

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PLATES 1–16

PLATE 1

Chondrocranium of *Thymallus arcticus*

A. Dorsal view, UMMZ 172465-S, about 1.7 ×

B. Ventral view, UMMZ 172465-S, about 1.7 ×

Abbreviations.—BOC, basioccipital; BS, basisphenoid; DF, dorsal fontanelle; EOC, exoccipital; EPO, epiotic; OPO, opisthotic; PF, prefrontal; PRO, prootic; PS, pterosphenoid; PTO, pterotic; SOC, supraoccipital; SPO, sphenotic.

A
PF
PS
SPO
DF
PTO
SOC
EPO
B
PF
PS
BS
SPO
PRO
PTO
BOC
EOC
OPO
EPO

PLATE 2

Chondrocranium of *Thymallus arcticus*

A. Lateral view, UMMZ 172465-S about 1.7 ×

B. Posterior view, UMMZ 172465-S about 1.7 ×

C. Mesial view, UMMZ 172465-S about 1.7 ×

Abbreviations.—BOC, basioccipital; BS, basisphenoid; DF, dorsal fontanelle; EOC, exoccipital; EPO, epiotic; FM, foramen magnum; OPO, opisthotic; PF, prefrontal; PRO, prootic; PS, pterosphenoid; PTO, pterotic; SOC, supraoccipital; SPO, sphenotic.

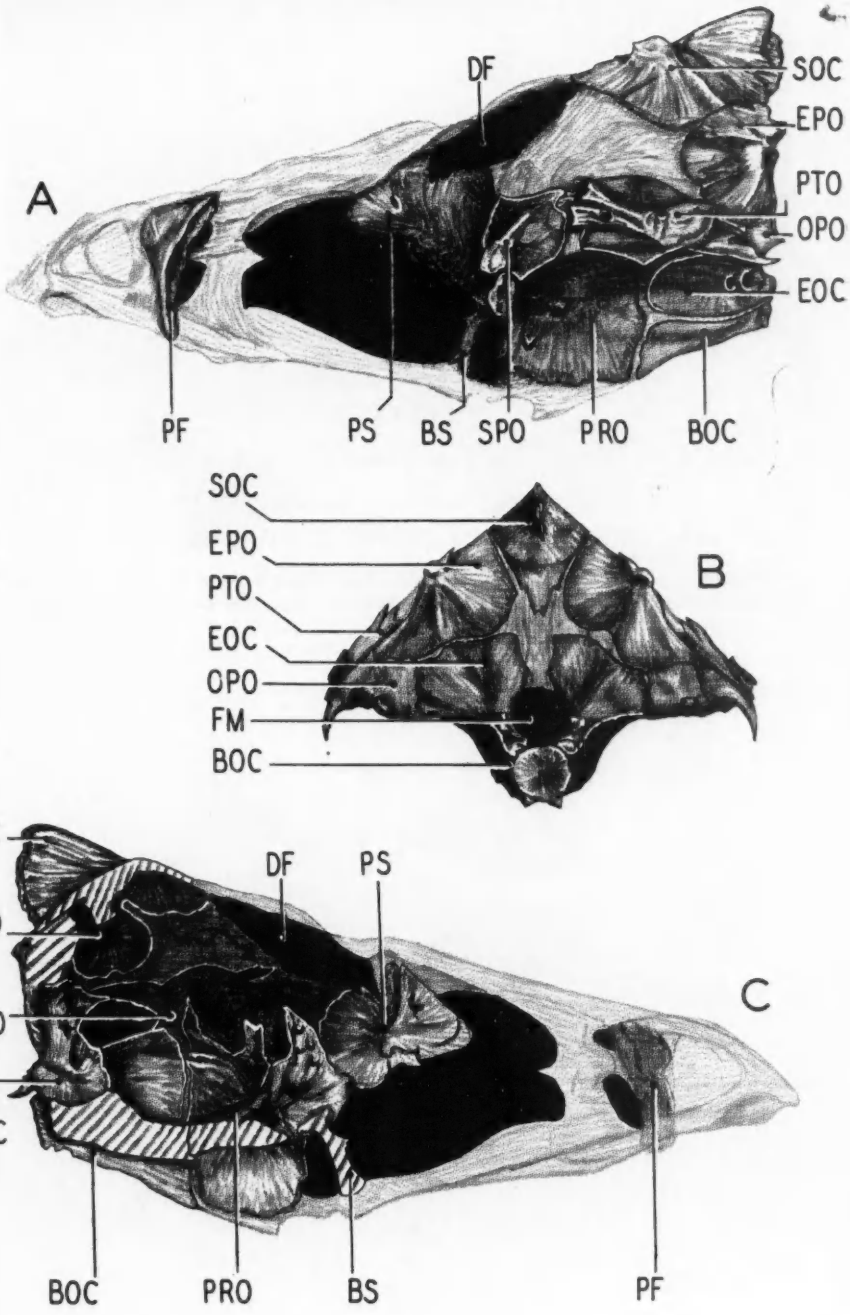

A
DF
SOC
EPO
PTO
OPO
EOC
PF
PS
BS
SPO
PRO
BOC
B
SOC
EPO
PTO
EOC
OPO
FM
BOC
C
SOC
DF
PS
EPO
PTO
EOC
BOC
PRO
BS
PF

PLATE 3

Dorsal views of chondrocrania of Salmonidae

A. *Coregonus artedii.* UMMZ 172466-S, about 1.6 ×

B. *Salvelinus namaycush.* UMMZ 172463-S, about 1.6 ×

Abbreviations.—DF, dorsal fontanelle; EOC, exoccipital; EPO, epiotic; HE, hypethmoid; OPO, opisthotic; PF, prefrontal; PS, pterosphenoid; PTO, pterotic; SOC, supraoccipital; SPO, sphenotic.

PF
PS
SPO
DF
PTO
SOC
EPO
OPO
EOC
B
A
HE
PF
PS
SPO
DF
PTO
SOC
EPO
OPO

PLATE 4

Dermal skull bones of *Thymallus arcticus*

UMMZ 172465-S, about 0.8 ×

Abbreviations.—A, angular; D, dentary; DS, dermosphenotic; ES, extrascapular; F, frontal; IO, infraorbital; IOP, interopercle; LA, lachrymal; M, maxilla; N, nasal; OP, opercle; P, parasphenoid; PA, parietal; PM, premaxilla; PO, postorbital; POP, preopercle; RA, retroarticular; SE, supraethmoid; SM, supramaxilla; SO, supraorbital; SOP, subopercle; V, vomer.

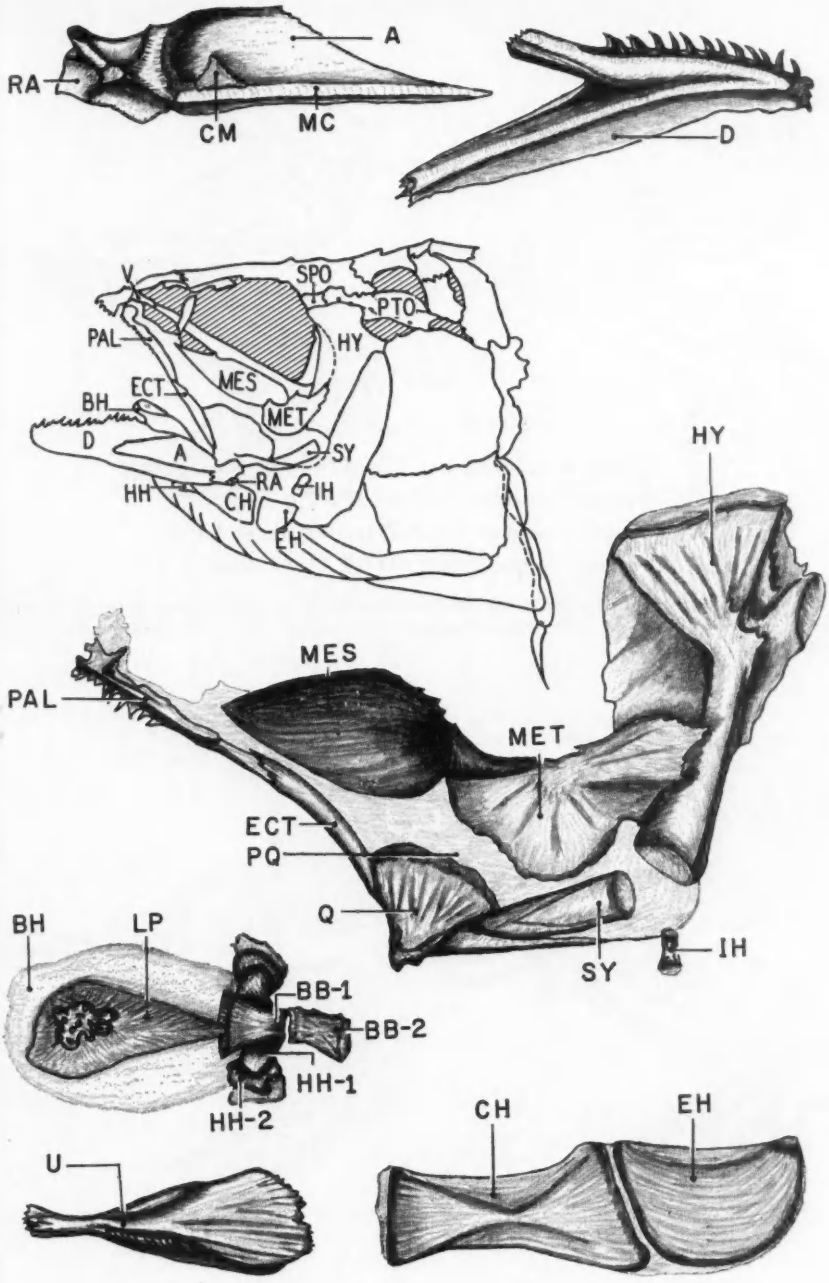
ES-3
ES-2
ES-1
OP
SOP
PA
DS
PO-3
PO-2
POP
IOP
SE
N
SO-I
SO-2
PM
F
PO-I
RA
IO
A
LA
SM
M
D
V
P

PLATE 5

Hyoid arch and lower jaw of *Thymallus arcticus*

UMMZ 172465-S, about 1.3 ×

Abbreviations.—A, angular; BB, basibranchial; BH, basihyal; CH, ceratohyal; CM, coronomeckelian; D, dentary; ECT, ectopterygoid; EH, epihyal; HH, hypohyal; HY, hyomandibular; IH, interhyal; LP, lingual plate; MC, Meckel's cartilage; MES, mesopterygoid; MET, metapterygoid; PAL, palatine; PQ, palatoquadrate; Q, quadrate; RA, retroarticular; SY, symplectic; U, urohyal.


A
RA
CM
MC
D
V
SPO
PTO
PAL
HY
MES
ECT
BH
MET
D
A
SY
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IH
HH
CH
EH
HY
MES
PAL
MET
ECT
PQ
Q
BH
LP
IH
SY
BB-1
BB-2
HH-1
HH-2
CH
EH
U

PLATE 6

Branchial skeletons of Salmonidae

A. *Prosopium cylindraceum*, UMMZ 59728, about 1.6 ×

B. *Salvelinus fontinalis*, UMMZ 85467, about 1.1 ×

C. *Thymallus arcticus*, UMMZ 167092, about 1.1 ×

D. *Coregonus clupeaformis*, UMMZ 75327, about 1.3 ×

Abbreviations.—BB, basibranchial; BP, basibranchial plate; CB, ceratobranchial; EB, epibranchial; HB, hypobranchial; HH, hypohyal; LP, lingual plate; PB, pharyngobranchial; PP, pharyngeal plate.

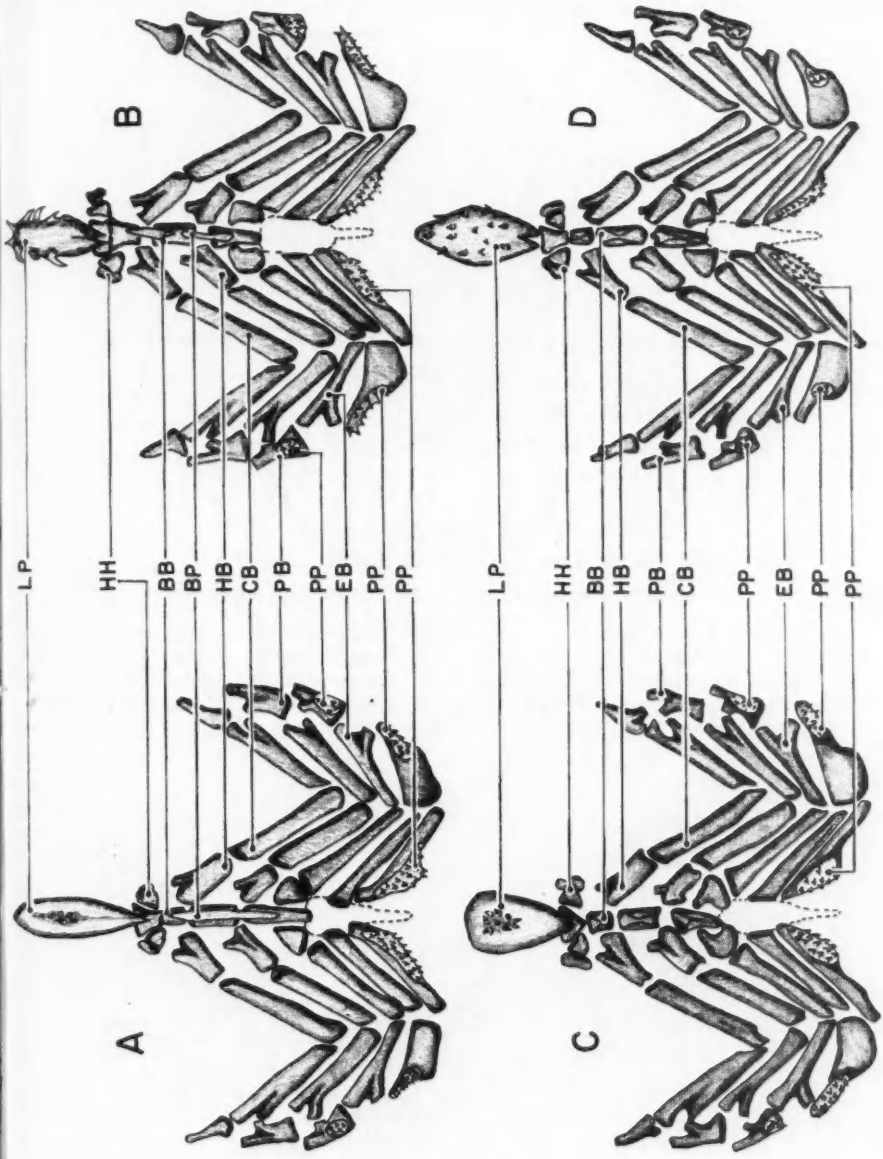

A
B
C
D
LP
HH
BB
BP
HB
CB
PB
PP
EB
PP
PP

PLATE 7

Axial skeleton and pelvic girdle of *Thymallus arcticus*

A. Trunk vertebrae nos. 8, 9, and 10, UMMZ 167092, about 1.3 ×

B. Caudal vertebrae nos, 45, 46, 47, and 48, Ptergiophores of anal fin nos. 9, 10, 11, and 12, Anal fin rays nos. 11, 12, 13, 14, and 15, UMMZ 167092, about 1.4 ×

C. Caudal skeleton, UMMZ 167092, about 1.4 ×

D. Pelvic girdle, UMMZ 167092, about natural size

Abbreviations.—AFR, anal fin ray; BPTG, basipterygium; C, centrum; E. epural; EHS, expanded haemal spine; EN, epineural; ENS, expanded neural spine; EP, epipleural; H, hypural; HA, haemal arch; HS, haemal spine; IN, interneural; NA, neural arch; NS, neural spine; PAP parapophysis; PFR, pelvic fin ray; POZ, postzygapophysis; PRZ, prezygapophysis; PTG, pterygiophore; R, rib; UN, uroneural; US, urostyle.

A
IN
NS
NA
EN
PAP
EP
R
C
B
PRZ
PRZ
POZ
POZ
HA
HS
C
UN-1
E-1
E-2
UN-2
US
UN-3
7
6
5
4
H
3
2
1
EHS
ENS
PTG-3
PTG-2
PTG-1
AFR
D
BPTG
PFR

PLATE 8

Pectoral girdle of *Thymallus arcticus*

A. Mesial view, UMMZ 172465, about 0.4 ×

B. Lateral view, UMMZ 172465, about 0.4 ×

Disarticulated skeleton, UMMZ 167092, about 2.6 ×

Abbreviations.—AC, actinost; CC, coracoid; CL, cleithrum; MSC, mesocoracoid; PCL, postcleithrum; PT, posttemporal; S, scapula; SCL, supracleithrum.

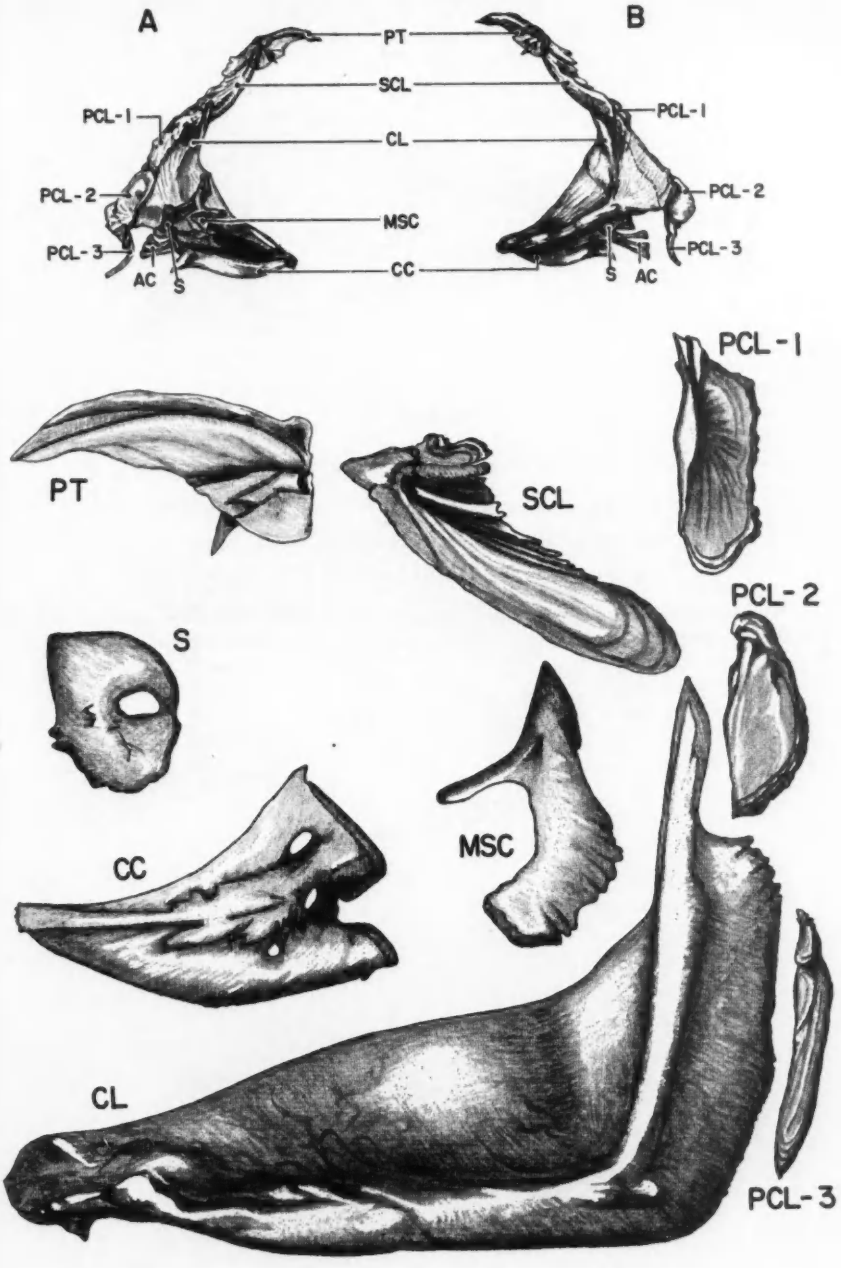

A
B
PT
SCL
PCL-1
CL
PCL-2
MSC
PCL-3
CC
AC
S
PCL-1
PT
SCL
PCL-2
S
MSC
CC
CL
PCL-3

PLATE 9

Dorsal view of skulls of Salmonidae

A. *Thymallus arcticus*, UMMZ 172465-S, about 0.8 ×

B. *Salvelinus namaycush*, UMMZ 172463-S, about 0.7 ×

C. *Coregonus artedii*, UMMZ 172467-S, about 0.9 ×

Abbreviations.—DS, dermosphenotic; ES, extrascapular; F, frontal; PA, parietal; PM, premaxilla; PT, posttemporal; PTO, pterotic; SE, supraethmoid; SO, supraorbital.

PT
ES
PA
PTO
DS
F
SO-I
SE
PM
A
B
C

PLATE 10

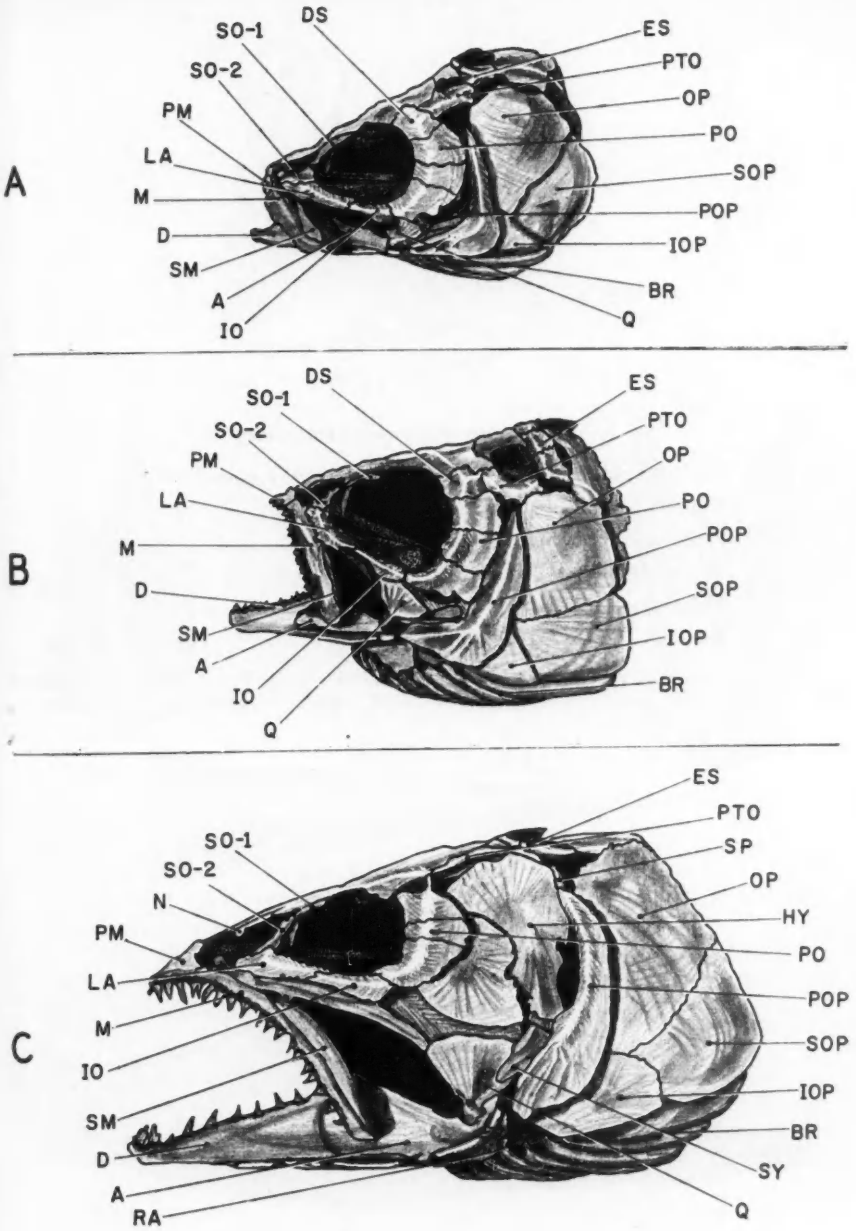
Lateral views of skulls of Salmonidae

A. *Coregonus artedii*, UMMZ 172467-S, about 0.36 ×

B. *Thymallus arcticus*, UMMZ 172465-S, about 0.36 ×

C. *Salvelinus namaycush*, UMMZ 172464-S, about 0.27 ×

Abbreviations.—A, angular; BR, branchiostegal ray; D, dentary; DS, dermosphenotic; ES, extrascapular; HY, hyomandibular; IO, infraorbital; IOP, interopercle; LA, lachrymal; M, maxilla; N, nasal; OP, opercle; PM, premaxilla; PO, postorbital; POP, preopercle; PTO, pterotic; Q, quadrate; RA, retroarticular; SM, supramaxilla; SO, supraorbital; SOP, subopercle; SP, suprapreopercle; SY, symplectic.


A
DS
SO-1
SO-2
PM
LA
M
D
SM
A
IO
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PTO
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PO
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IOP
BR
Q
B
DS
SO-1
SO-2
PM
LA
M
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OP
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POP
SOP
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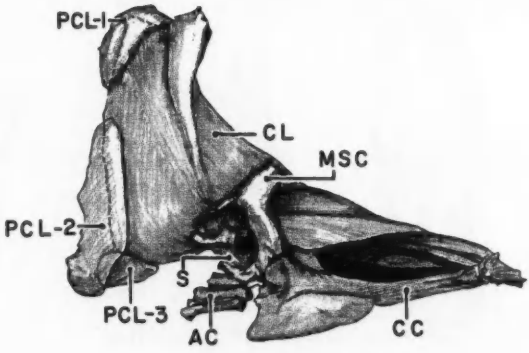
IOP
BR
SY
Q

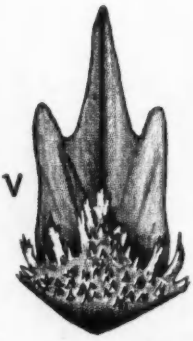
PLATE 11

Selected bones of *Stenodus leucichthys*

Pectoral girdle, mesial view, UMMZ 172487, about 0.6 ×
Vomer, UMMZ 161995, about 2.0 ×
Premaxilla, UMMZ 161995, about 2.0 ×
Supraethmoid, UMMZ 161995, about 2.0 ×
Palatine, UMMZ 161995, about 2.0 ×
Dentary, UMMZ 161995, about 1.5 ×

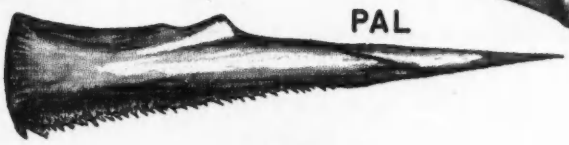
Abbreviations.—AC, actinost; CC, coracoid; CL, cleithrum; D, dentray; MSC, mesocoracoid; PAL, palatine; PCL, postcleithrum; PM, premaxilla; S, scapula; SE, supraethmoid; V, vomer.


PCL-1
CL
MSC
PCL-2
S
PCL-3
AC
CC


V

PM

SE


PAL

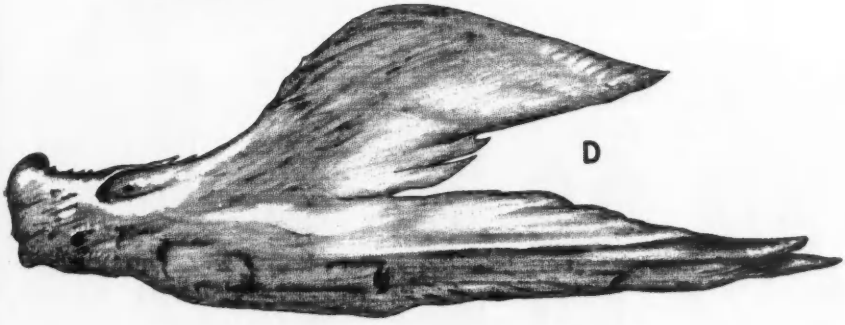
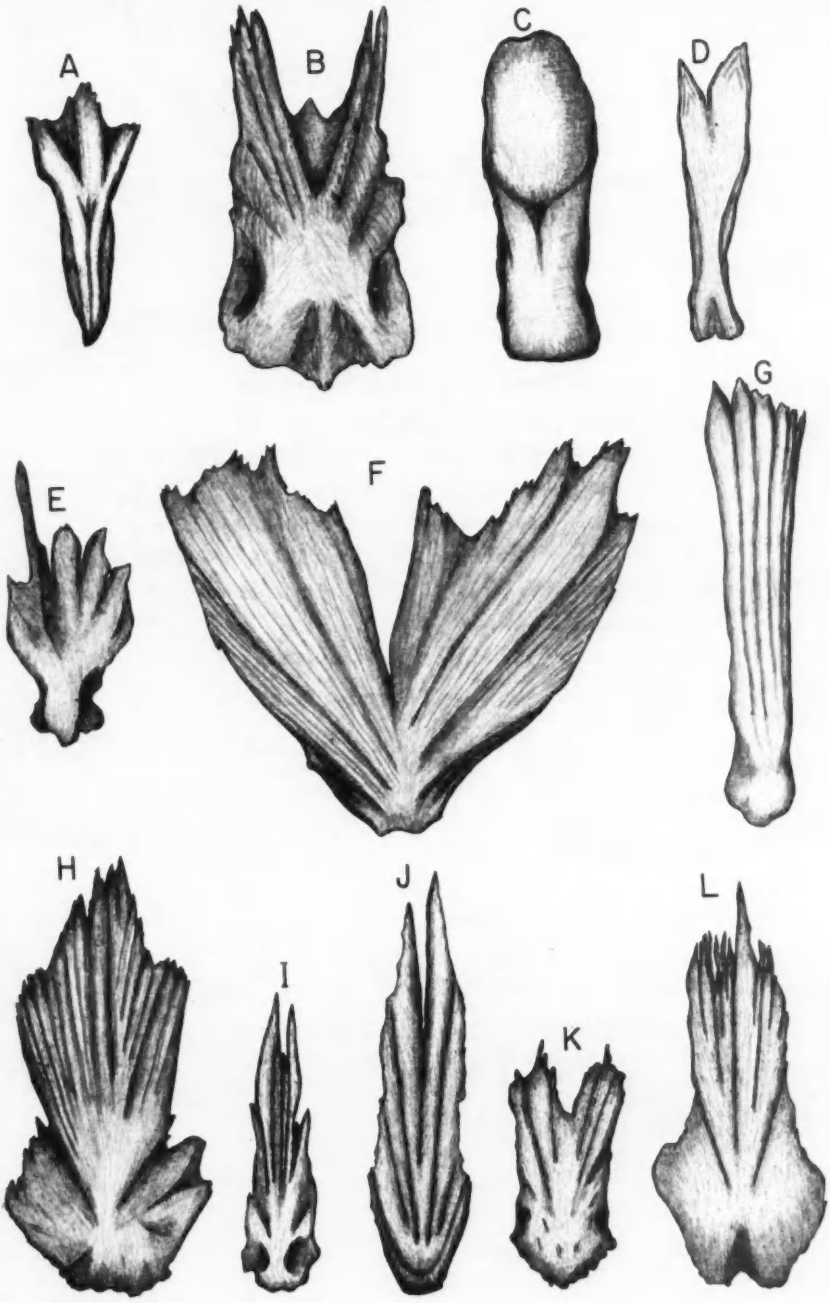

D

PLATE 12

Supraethmoid bones of Salmonidae

A. *Coregonus clupeaformis*, UMMZ 75327, about 4.0 ×
B. *Coregonus artedii*, UMMZ 172467, about 3.2 ×
C. *Prosopium cylindraceum*, UMMZ 59702, about 2.8 ×
D. *Prosopium abyssicola*, UMMZ 141811, about 3.0 ×
E. *Coregonus sardinella*, about 3.3 ×
F. *Oncorhynchus gorbuscha*, UMMZ 172444, about 1.7 ×
G. *Prosopium gemmiferum*, UMMZ 141809, about 3.6 ×
H. *Hucho perryi*, UMMZ 172493, about 1.3 ×
I. *Brachymystax lenok*, UMMZ 172490, about 1.8 ×
J. *Salvelinus namaycush*, UMMZ 172463, about 2.0 ×
K. *Salmo gairdneri*, UMMZ 172468, about 1.7 ×
L. *Salvelinus fontinalis*, UMMZ 172462, about 1.7 ×


A
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L

PLATE 13

Upper jaw bones of Salmonidae

A. *Coregonus nasus*, about 1.1 ×
B. *Prosopium gemmiferum*, UMMZ 156788, about 1.1 ×
C. *Salmo trutta*, UMMZ 124553, about 1.9 ×
D. *Brachymystax lenok*, UMMZ 172490, about 1.1 ×
E. *Prosopium cylindraceum*, UMMZ 59728, about 1.9 ×
F. *Stenodus leucichthys*, UMMZ 161995, about 0.6 ×
G. *Coregonus sardinella*, about 1.1 ×
H. *Hucho perryi*, UMMZ 172493, about 0.8 ×

Abbreviations.—M, maxilla; PM, premaxilla; SM, supramaxilla.

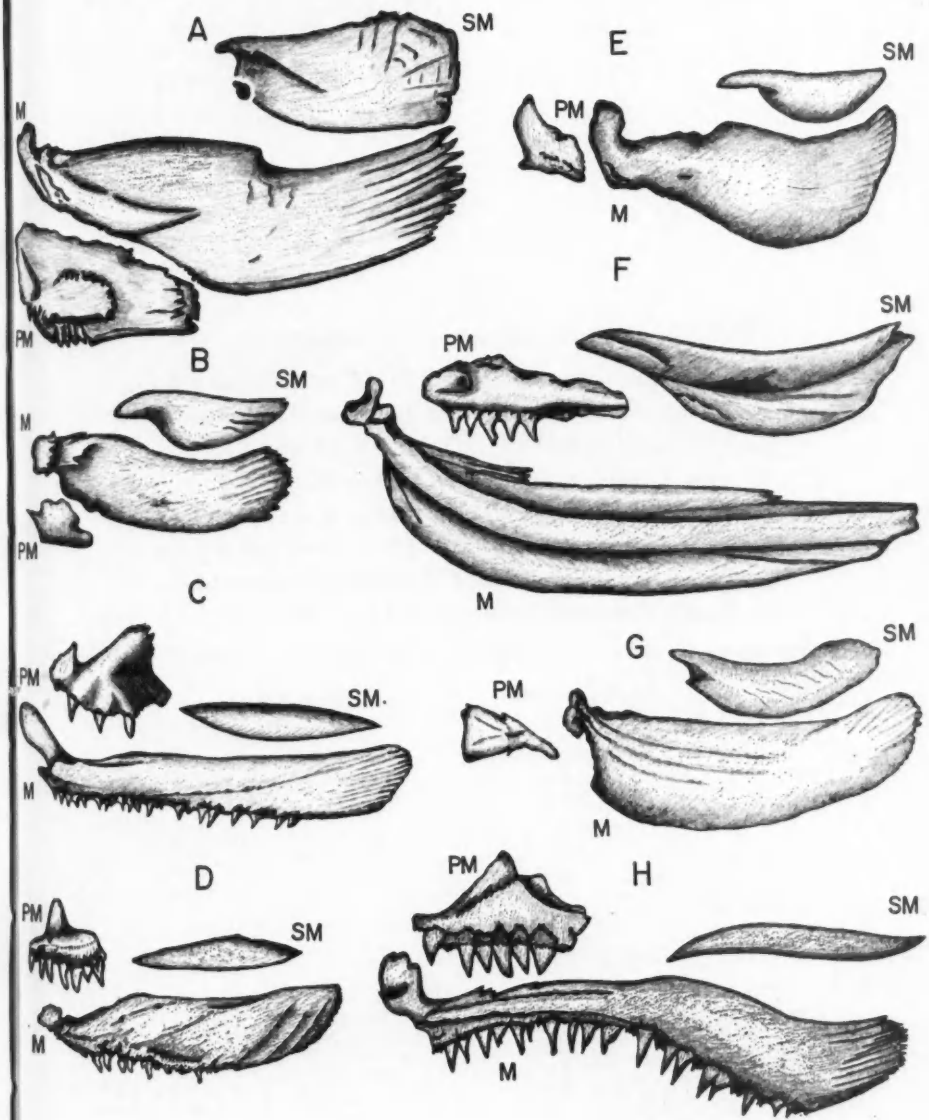
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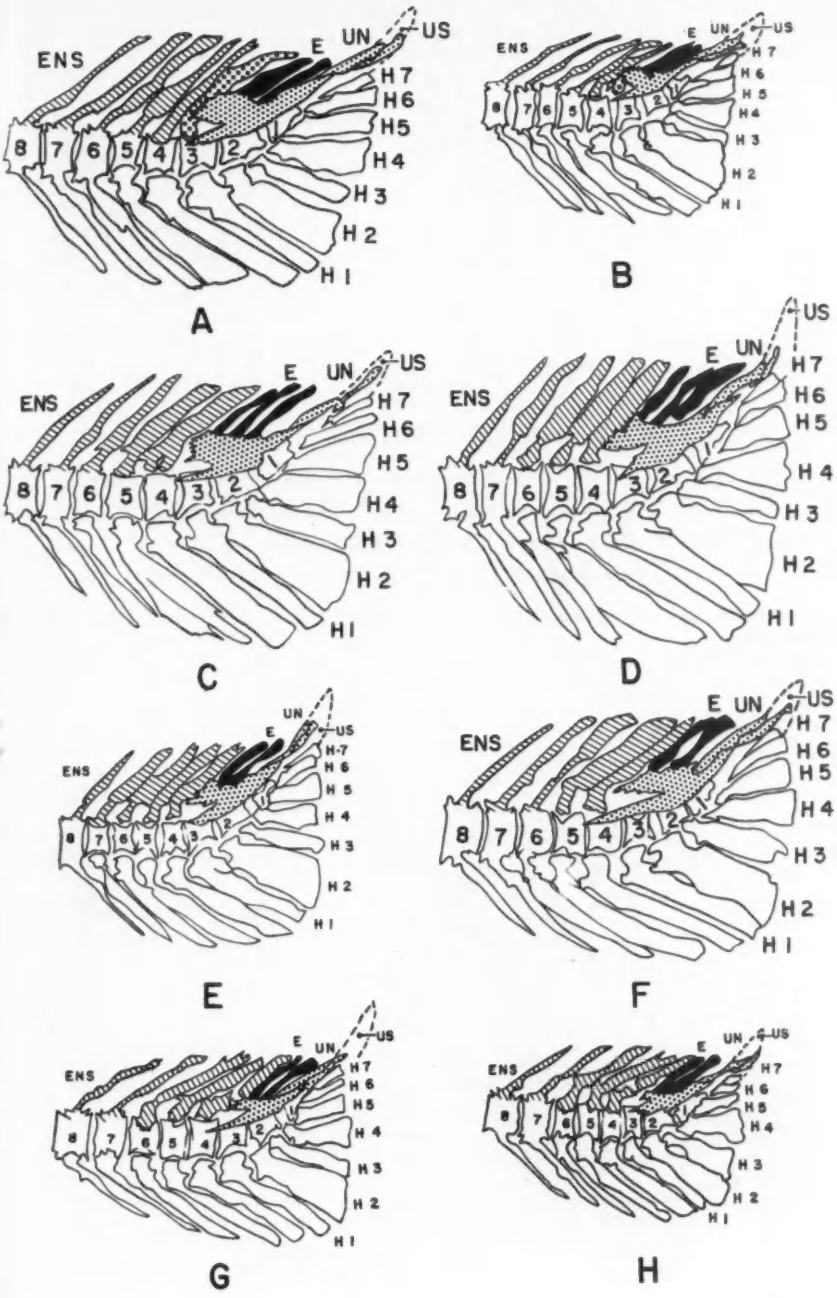
PLATE 14

Caudal skeletons of Salmonidae

A. Type 1, *Salvelinus fontinalis*, UMMZ 69641, about 4.6 ×
B. Type 2, *Salvelinus namaycush*, UMMZ 162155, about 3.6 ×
C. Type 3, *Salmo gairdneri*, UMMZ 127601, about 5.1 ×
D. Type 3, *Salmo trutta*, UMMZ 124553, about 4.1 ×
E. Type 4, *Salmo trutta*, UMMZ 124553, about 3.6 ×
F. Type 4, *Salmo salar*, UMMZ 141019, about 4.6 ×
G. Type 5, *Coregonus artedii*, UMMZ 145300, about 3.1 ×
H. Type 5, *Prosopium coulteri*, UMMZ 167954, about 3.1 ×

Abbreviations.—E, epural; ENS, expanded neural spine; H, hypural; UN, uroneural; US, urostyle.


ENS
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UN
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H7
H6
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H4
H3
H2
H1
8
7
6
5
4
3
2
A
B
C
D
E
F
G
H

PLATE 15

Caudal skeletons of Salmonidae and Elopidae

A. Type 6, *Oncorhynchus tshawytscha*, UMMZ 146364, about 4.3 ×

B. Type 5, *Thymallus arcticus*, UMMZ 169574, about 4.9 ×

C. Type 6, *Hucho perryi*, UMMZ 172490, about 2.4 ×

D. *Elops affinis*, UMMZ 159257, about 2.8 ×

Abbreviations.—E, epural; ENS, expanded neural spine; H, hypural; UN, uroneural; US, urostyle.

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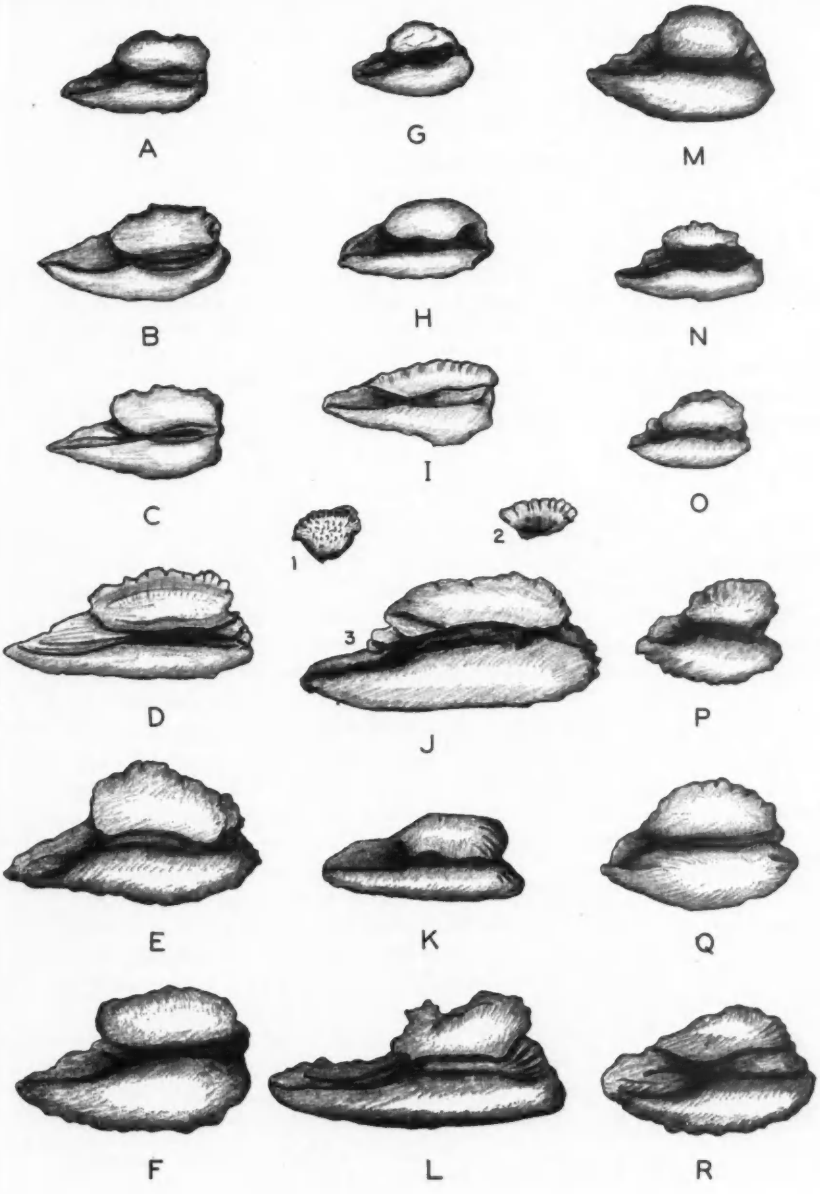
PLATE 16

Otoliths of Salmonidae

A. *Coregonus kiyi*, UMMZ 172477-S, 1.0 ×
B. *Coregonus reighardi*, UMMZ 172476-S, 1.6 ×
C. *Coregonus alpenae*, UMMZ 172475-S, 1.6 ×
D. *Coregonus artedii*, UMMZ 172467-S, 1.9 =
E. *Prosopium cylindraceum*, UMMZ 52880, 2.6 ×
F. *Coregonus hoyi*, UMMZ 172479-S, 2.6 ×
G. *Salvelinus namaycush*, UMMZ 172463, 1.0 ×
H. *Prosopium coulteri*, UMMZ 167954, 2.6 ×
I. *Coregonus clupeaformis*, UMMZ 54314, 1.3 ×
J. *Thymallus arcticus*, UMMZ 172465-S
   1 Lapillus, 2.9 ×
   2 Asteriscus, 2.9 ×
   3 Sagitta, 2.9 ×
K. *Prosopium gemmiferum*, UMMZ 141809, 2.6 ×
L. *Stenodus leucichthys*, UMMZ 172487-S, 1.6 ×
M. *Salvelinus fontinalis*, UMMZ 172462-S, 2.3 ×
N. *Salmo trutta*, UMMZ 172470-S, 1.0 ×
O. *Oncorhynchus keta*, UMMZ 172452-S, 1.6 ×
P. *Oncorhynchus nerka*, UMMZ 172443-S, 1.6 ×
Q. *Salmo gairdneri*, UMMZ 172468-S, 2.3 ×
R. *Oncorhynchus gorbuscha*, UMMZ 172444-S, 2.9 ×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R

A Systematic Study of the *Salvelinus alpinus* Complex in North America[1,2]

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Institute of Fisheries, University of British Columbia
Vancouver, B.C.

ABSTRACT

Sympatric populations of *Salvelinus malma* and *Salvelinus alpinus* from Karluk and Fraser Lakes, Kodiak Island, Alaska, were compared using the discriminant function analysis. The analysis indicated that hybridization between *S. malma* and *S. alpinus* rarely, if ever, occurs in these lakes. Therefore, *S. malma* and *S. alpinus* are considered distinct species. Data on 507 *S. malma* and 411 *S. alpinus* from 77 localities suggest at least two distinct forms of both *S. malma* and *S. alpinus* in North America. Speculations are made on the origin and evolution of *S. malma* and *S. alpinus*.

INTRODUCTION

The chars (*Salvelinus*) form a holarctic genus of salmonid fishes. Morphologically chars are very plastic; stunted populations and colour variants are common. As a result numerous species of *Salvelinus* have been described, many of which are probably synonymous. The present study is an attempt to clarify the systematics of the *Salvelinus alpinus* complex in North America (excluding Greenland). Particular attention is paid to the systematic position of the Dolly Varden, *Salvelinus malma*.

Jordan, Evermann and Clark (1930) list 13 species of *Salvelinus* from North America. These chars fall into three distinct groups: *S. namaycush*, *S. fontinalis*, and the *S. alpinus* group. Most authors now consider each of the first two groups as single species endemic to North America. The third group is circumpolar in distribution, and contains an undetermined number of species. This group is referred to as the Arctic chars, or the "*S. alpinus* complex." Berg (1948) recognizes 11 species of Arctic chars from Russia. Jordan *et al.* (1930) list 4 species of Arctic chars from Greenland and the Canadian arctic. Vladykov (1954) and Walters (1955) suggest the use of the single name *Salvelinus alpinus* for the whole group until more material is available for study.

A char closely related to the *S. alpinus* complex is distributed along the Pacific coasts of North America and Asia. This is the Dolly Varden, *Salvelinus malma* (Walbaum). Several authors (Dymond, 1936, 1947; Carl and Clemens, 1953; Lindsey, 1956) have considered the Dolly Varden a part of the *S. alpinus* complex and refer to it by the subspecific name *Salvelinus alpinus malma*. Other

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[2]Based on a thesis submitted to the University of British Columbia in partial fulfilment of the requirements for the degree of Master of Science.
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Printed in Canada.

authors (Delacy and Morton 1943, Morton and Miller 1954) consider the Dolly Varden a distinct species, *Salvelinus malma*.

In the following discussion the names *S. alpinus* and *S. malma* are used for the North American species. The author believes these chars are conspecific with the European and Asian chars of the same names. However, no attempt has been made here to equate North American chars with European or Asian species. Where possible, comparisons are made, but due to the inadequacy of published material such comparisons are speculative.

Descriptions of North American *S. malma* and *S. alpinus* are included to facilitate possible future comparisons with European and Asian species. The data on which the following study is based are summarized in an Appendix.

MATERIALS AND METHODS

This study is based on examination of specimens from Washington, British Columbia, Yukon Territory, the Northwest Territories, and Alaska. Material from Alaska, Yukon Territory and northern British Columbia was largely collected during the summers of 1957, 1958 and 1960; *S. alpinus* from the Northwest Territories were principally obtained during the 1959 Barren Grounds Survey of the Arctic Unit of the Fisheries Research Board. The specimens are now in the museums of the Institute of Fisheries of the University of British Columbia, the College of Fisheries of the University of Washington, and the Royal Ontario Museum. Specimens from 77 localities, totalling 507 *S. malma* and 411 *S. alpinus*, were examined. Individuals ranged from 20 to 500 mm in length. Both anadromous and non-migratory populations were sampled.

All meristic counts and measurements follow Hubbs and Lagler (1958). Counts of fin rays, branchiostegal rays and vertebrae were made on cleared specimens under a binocular microscope. Most vertebral counts were made from radiographs. Gill rakers were counted by dissecting out the gill arch and counting the rakers under a binocular microscope. Pyloric caeca were counted as each caecum was detached from the main mass of caeca under a binocular microscope. Gill rakers and pyloric caeca were counted on all specimens examined.

The following measurements were made: fork length, head length, maxillary length, eye diameter, least caudal peduncle depth, and interorbital width.

The numbers of teeth on the tongue and on the basibranchial bones were counted. Tooth counts were made only on cleared and stained specimens. Alveoli from which teeth had been lost were included.

The numbers of spots in the area under the dorsal fin and above the lateral line were counted. Any spots partially in this area were included. Spots were counted only on fish on which the number of spots could be determined accurately. The horizontal diameter of the largest spot touching the lateral line was used as a measure of spot size. Spot size and spot number were found to vary with length and are of little taxonomic value.

The number of gill rakers, the number of pyloric caeca and the pores along the lateral line were found to be the most valuable characters for comparing

S. malma and *S. alpinus*. Vladykov (1954) has criticized the use of gill rakers in char taxonomy. He contends that the number of gill rakers varies with length in char. Correlation coefficients were calculated between length and: number of gill rakers, number of pyloric caeca, and number of pores along the lateral line. In each case, for both species, the correlation was non-significant and quite small (Table I). Therefore, Vladykov's criticism is invalid for these species, and all three characters can be used on specimens within the size range examined.

TABLE I. Correlation (r) of gill rakers, pyloric caeca, and pores along the lateral line with fork length in Karluk Lake *S. malma* and *S. alpinus*, together with the degrees of freedom (d.f.) and probability of significance (P).

	S. malma—33 specimens			*S. alpinus*—32 specimens		
	r	d.f.	P	r	d.f.	P
Gill rakers lower arch	0.11	31	>0.10	0.26	30	>0.10
Pyloric caeca	0.12	31	>0.10	0.25	30	>0.10
Pores along the lateral line	0.25	31	>0.10	0.24	30	>0.10

TREATMENT OF DATA

All body measurements were plotted against fork length or head length on logarithmic axes (Martin, 1949). These curves showed some differences in the relative growth rates of various body parts for *S. malma* and *S. alpinus*, but none of the differences were sufficient to characterize either species.

Significance of correlations between enumerated characters and length were tested using the correlation coefficient (Snedecor, 1956).

A discriminant function analysis (Fisher, 1936; Rao, 1952) was used on data from two Alaskan collections of char. The computations were done at the University of British Columbia computing centre on an Alwac IIIE computor. Discriminant function analysis is a technique for combining the discriminating power of several characters into a single discriminant score. Hubbs and Kuhne (1937) devised a character index which combined the numerical values of several characters into a single expression. Two major criticisms can be made of the Hubbs character index. Firstly, all of the characters are given equal weight, and secondly, no attempt is made to determine whether the characters combined are correlated. Combining characters into an index without weighting the characters assumes that all of the characters used are of equal value in distinguishing the particular form. This is not always so. Combining correlated characters can produce a biased index. Correlated characters should be combined as a group rather than treated individually.

The discriminant function analysis overcomes both of these objections. Each character is weighted according to the difference between the means of that character for both populations and also for the total variation of the character. The characters that best separate the populations are automatically given the greatest weight. If some of the characters are correlated the best of the correlated

characters is weighted like any other character, and characters correlated with it are given weight only as they contribute to discrimination beyond that provided by their correlate.

This type of analysis requires some preliminary estimate of the differences that exist between the means of the various characters in each of the two populations, necessitating a preliminary division into two groups. The differences thus established are then used to provide statistics for the calculation of a discriminant function that will best combine the various characters to maximize the difference between the two groups. The technique for calculating discriminant scores is given by Rao (1952).

TAXONOMIC RELATIONSHIP OF *SALVELINUS MALMA* AND *SALVELINUS ALPINUS*

To determine whether *S. malma* is a distinct species, or a subspecies of *S. alpinus*, it is necessary to examine samples from areas where the two forms occur together. Several such areas were sampled.

Karluk Lake

Karluk Lake is situated on Kodiak Island in the Gulf of Alaska. DeLacy and Morton (1942) reported two closely related species of *Salvelinus* from Karluk Lake. They assigned one species to the *S. alpinus* complex and, because the two forms occur in the same lake, they regarded the other as a distinct species *S. malma*. They presented a morphometric and meristic comparison. Examination of their data reveals no characters that can completely separate the two nominal species in Karluk Lake. All of the characters presented showed some degree of overlap.

If the two forms of chars are distinct species, the overlap in all of the characters examined suggests that introgressive hybridization might occur in Karluk Lake. DeLacy and Morton did not consider hybrids in their discussion.

In June 1958, 65 specimens of *Salvelinus* were collected by the author from Karluk Lake. All collections were made by gill nets or seines. Field observation suggested two types of chars in Karluk Lake. One type was characterized by numerous small, yellowish-red spots, and the other by fewer, larger, bluish-red spots. A few adults and most juveniles could not be distinguished by colour pattern.

The only other character that suggested two populations was the number of gill rakers. The number of gill rakers on the lower limb of the first arch (Fig. 1) has a distinctly bimodal distribution when the entire Karluk Lake sample is plotted. Numbers of males and females are approximately equal in both peaks.

For the preliminary segregation of the sample necessary to provide an estimate of differences in the means the gill raker count was used, for the following reasons. DeLacy and Morton (1942) found that in Karluk Lake the number of gill rakers on the lower limb of the first arch ranged from 8–12 in the *S. malma* form and from 12–15 in the *S. alpinus* form. Also, examination of *S. malma*

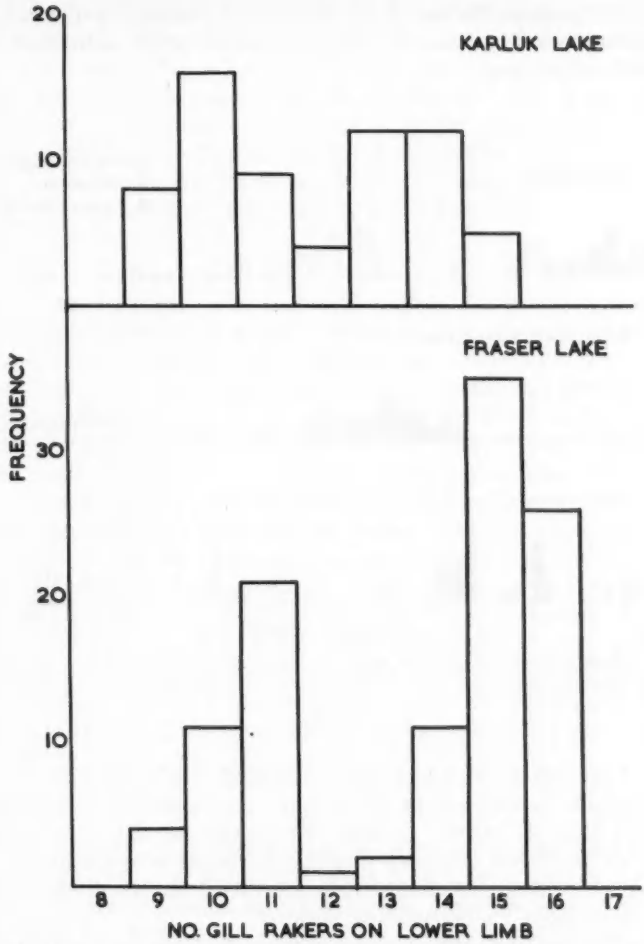

FIG. 1. Distribution of gill rakers on the lower limb of the first arch for the entire Karluk and Fraser Lake samples.

from other nearby areas where only *S. malma* occurs confirmed that the range of gill rakers on the lower limb is from 8–12. Accordingly, the entire Karluk Lake sample was segregated into "*S. malma*"[4] and "*S. alpinus*" on this basis, with the exception of specimens with 12 gill rakers which were included in both groups. The characters used in the discriminant analysis were: gill rakers, pyloric caeca and pores along the lateral line.

[4]The validity of *S. malma* has not yet been discussed. "*S. malma*" and "*S. alpinus*" are used here for convenience in referring to the two forms of Karluk char.

Figure 2a presents the calculated discriminant scores for the Karluk Lake sample. Two discrete groups are indicated, with a single individual occupying an intermediate position.

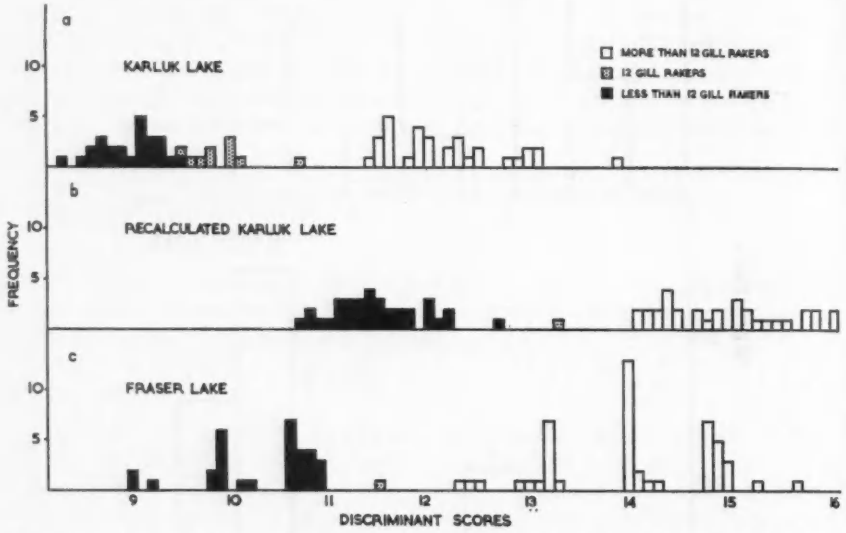

FIG. 2. (a) Distribution of discriminant scores for the Karluk Lake sample. (b) Recalculated Karluk Lake discriminant scores. (c) Distribution of discriminant scores for the Fraser Lake sample.

Eight of the individuals which had intermediate gill raker counts, and which had been included in both groups in the first calculation, can be seen in Fig. 2a to lie within the "*S. malma*" group. Therefore, the eight individuals were reclassified as "*S. malma*" and new discriminant scores were calculated. Figure 2b presents the recalculated discriminant scores for Karluk Lake. The same specimen still occupies an intermediate position.

In spot number and pyloric caeca number the intermediate individual in Fig. 2b is near the mode for "*S. alpinus*" and at the extreme range of Karluk "*S. malma*". DeLacy and Morton[5] give the range in vertebral counts for Karluk Lake char as 62–66 for "*S. malma*" and 65–69 for "*S. alpinus*"; the vertebral count for this individual is 66. Again the intermediate individual is near the mode for "*S. alpinus*" and at the extreme range of "*S. malma*". These facts suggest that the intermediate is "*S. alpinus*", but do not eliminate the possibility that it is a hybrid.

All of the specimens from Karluk Lake can be separated into two discrete groups, with one possible exception. However, there is still the objection that

[5]DeLacy and Morton (1943) did not include the last two vertebrae in their counts. Two vertebrae have been added to their counts to make them comparable.

differences observed might be phenotypic, a result of the anadromous behaviour of the population of "*S. malma*" in that lake. DeLacy and Morton noted major behaviour differences between the two Karluk Lake forms of *Salvelinus*. The "*S. malma*" form is anadromous while the "*S. alpinus*" form is non-migratory. This difference in environment might account for the morphometric differences between the adult forms in Karluk Lake, which could be anadromous and non-migratory populations of the same species. Fortunately it was possible to test this possibility with samples from a nearby land-locked lake.

Fraser Lake

Fraser Lake is a short distance east of Karluk Lake on Kodiak Island. It is completely land-locked by a 31-foot (10-metre) falls on the outlet stream.

In June, 1958, 92 specimens of *Salvelinus* were collected in Fraser Lake by gill nets and seine. As in Karluk Lake, gill raker number was the only character to show bimodality when the frequency distributions of the entire sample were plotted. For reasons discussed previously, the sample was segregated into "*S. malma*" and "*S. alpinus*" on the basis of the number of gill rakers on the lower limb of the first arch. The discriminating powers of the same four characters were again combined into a discriminant score. On this basis the specimens from Fraser Lake can be separated into two discrete groups (Fig. 2c). One individual has a somewhat intermediate score, but is much closer to the "*S. malma*" group than to the "*S. alpinus*" group. In spot number and spot size this individual lies within the range of both "*S. malma*" and "*S. alpinus*", but in both of these characters it is near the mean of the "*S. malma*" group and at the extreme range of the "*S. alpinus*" group. The vertebral count for this fish is 64, which is outside of the range for *S. alpinus* in Karluk Lake. These facts suggest that the intermediate is "*S. malma*".

Kenai River

Two specimens were collected from Kenai River on the Kenai Peninsula, Gulf of Alaska. One char had 12 gill rakers on the lower limb of the first arch, 27 pyloric caeca and numerous small spots. The other char had 13 gill rakers on the lower limb, 32 pyloric caeca and fewer, larger spots. These two Kenai fishes probably represent "*S. malma*" and "*S. alpinus*" respectively.

Lake Aleknagik and Tributaries

Lake Aleknagik is the first in a series of lakes at the headwaters of the Woods River, which enters Bristol Bay near Dillingham, Alaska. Samples were obtained from the lake and from Hansen Creek, a small tributary entering the east side about 3 miles north of the lake outlet.

Table II presents a comparison of adult char collected in Lake Aleknagik and in Hansen Creek. Judging from the Karluk and Fraser Lakes samples the number of gill rakers on the lower limb of the first arch is the best morphological difference between "*S. malma*" and "*S. alpinus*". The mean number of gill rakers

TABLE II. Comparison of chars from Lake Aleknagik and Hansen Creek (based on 30 specimens from each locality).

	Lake Aleknagik		Hansen Creek	
	Range	Mean	Range	Mean
Gill rakers lower limb	12–17	15.1	11–14	12.9
Pyloric caeca	29–74	52.5	21–30	26.7
Vertebrae	66–71	67.6	66–70	67.6

on the lower limb in the Lake Aleknagik sample is 15.1, with a range of 12–17. This, and all other characters examined, indicate that the Lake Aleknagik sample represents "*S. alpinus*".

The Hansen Creek sample is less easy to classify. Table I shows that, by Karluk and Fraser Lake standards, the Hansen Creek fish resemble "*S. alpinus*" in vertebral count, resemble "*S. malma*" in caecal count, and are intermediate in gill raker number. The spot pattern of the Hansen Creek fish suggests "*S. malma*", but the fish are small and spot size and number are correlated with length. The Hansen Creek sample is therefore intermediate between "*S. malma*" and "*S. alpinus*" in gill raker number, but like "*S. alpinus*" in number of vertebrae, and like "*S. malma*" in number of pyloric caeca.

There are several possible explanations for the Hensen Creek chars. They may be a dwarf, stream-dwelling population of the "*S. alpinus*" which occur in Lake Aleknagik. In this case the unusual number of gill rakers and pyloric caeca might be the result of the stream environment. However, dwarf, stream-dwelling *S. alpinus* from Baffin Island have the same number of gill rakers and pyloric caeca as normal *S. alpinus* from the same area (Table III). This suggests

TABLE III. Comparison of dwarf and normal *S. alpinus* from Baffin Island (10 specimens from each locality).

	Dwarf chars Sapuladjuk		Normal chars Nettilling Lake	
	Range	Mean	Range	Mean
Gill rakers lower limb	14–17	16	14–17	16
Pyloric caeca	32–47	38	29–46	38

that the unusual meristic counts of the Hansen Creek chars are not the result of environment. The Hansen Creek chars probably represent a genetically distinct form of *Salvelinus*.

Another possible explanation of the Hansen Creek chars is that they are the result of hybridization between "*S. malma*" and "*S. alpinus*". Hubbs (1955) suggests that interspecific hybrids in fishes are usually intermediate in all characters in which those species differ. The Hansen Creek chars are intermediate in the number of gill rakers, but not in other meristic characters. Ecologically the Hansen Creek chars appear to be closer to "*S. malma*" than to "*S. alpinus*". They are not known to occur in the lake, and apparently spawn in the stream.

The present author considers the Hansen Creek chars a form of "*S. malma*". The problem is discussed further in the section on the validity of subspecies in *S. malma*.

Brooks Lake and Tributaries

Brooks Lake is located on the Alaska Peninsula and drains into Bristol Bay by the Naknek River. In 1958 a sample of 21 char was collected from Brooks Lake and its tributaries by Mr T. Merrill of the United States Fish and Wildlife Service. Twenty of the char were from tributaries and one from Brooks Lake proper.

The single specimen from Brooks Lake has 14 gill rakers on the lower limb of the first arch, 43 pyloric caeca, and is undoubtedly "*S. alpinus*". The 20 fish from tributary streams have a mean of 12.6 gill rakers on the lower limb, with a range of 11–14. In this character they are intermediate between "*S. malma*" and "*S. alpinus*". The vertebral count of the sample from the tributaries ranges from 67–69 with a mean of 68, and in this character it resembles "*S. alpinus*". The number of pyloric caeca for the tributary sample ranges from 21–36 with a mean of 27.9. In this character the tributary sample resembles "*S. malma*".

The sample from tributaries to Brooks Lake is very similar morphologically to the Hansen Creek sample and presents the same problem.

Salmon Lake and Tributaries

Salmon Lake is located on the Seward Peninsula and drains into the Bering Sea by the Pilgrim River. A sample of 31 chars was obtained from Salmon Lake and a clear tributary stream. One char was from the lake proper, and 30 were from the tributary stream.

The single char from Salmon Lake has 15 gill rakers on the lower limb of the first arch, and represents "*S. alpinus*". The sample from the tributary stream has a mean of 12.8 gill rakers on the lower limb, with a range of 11–14. The number of vertebrae range from 65–71, with a mean of 67.8. The number of pyloric caeca range from 24–31, with a mean of 28.

In all of the characters examined the chars from the tributary to Salmon Lake are similar to the chars from tributaries to Aleknagik and Brooks Lakes. They are considered to be the same form.

Summary of the Taxonomic Relationship of "*S. malma*" and "*S. alpinus*"

The validity of doubtful species pairs can be established if they occur sympatrically without mass hybridization. Occasional hybridization may occur, but as long as the hybrids are rare the species can be considered valid. In Karluk and Fraser Lakes *S. malma* and *S. alpinus* occur sympatrically. The evidence indicates that within these lakes hybridization between *S. malma* and *S. alpinus* rarely, if ever, occurs. The two specimens from Kenai River also appear to represent these two species. North of the Alaska Peninsula the distinction is not so clear, but in two Bristol Bay localities and one on the Seward

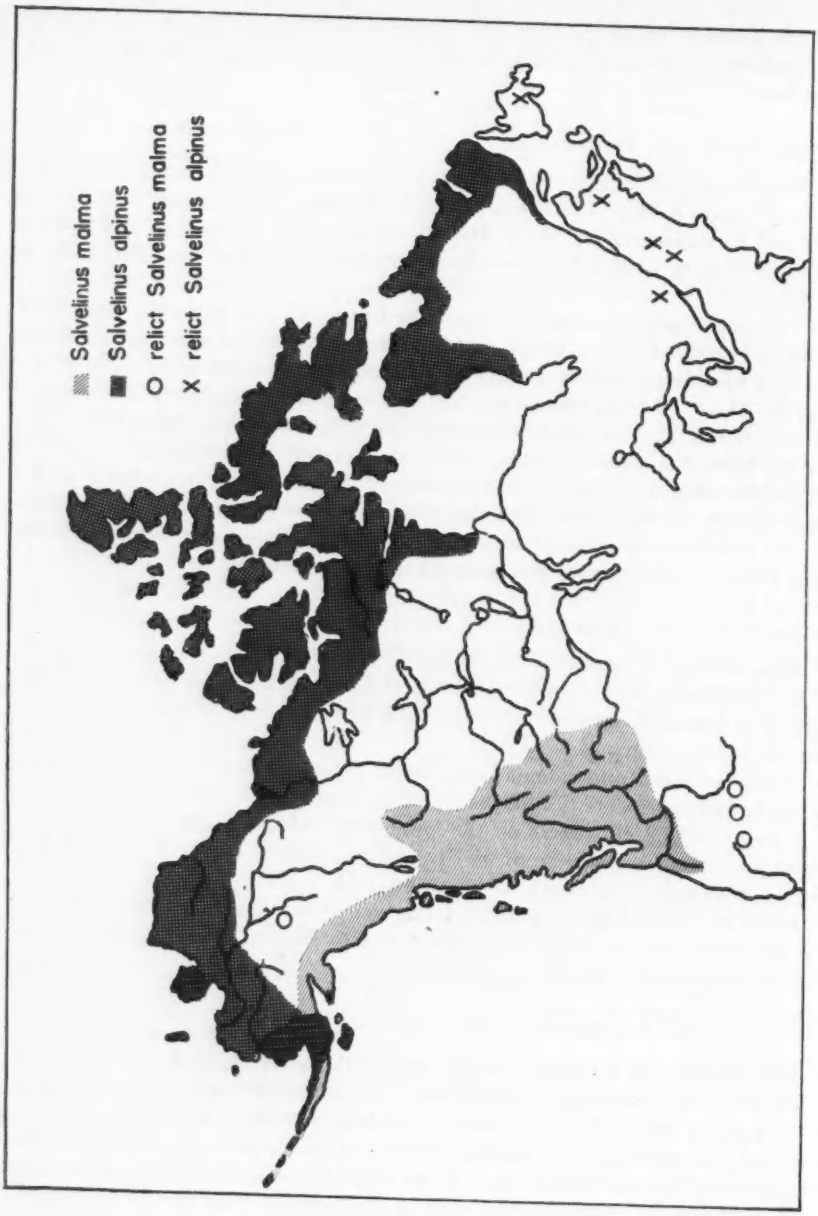

FIG. 3. North American distribution of *S. malma* and *S. alpinus*.

Peninsula a common pattern is evident. In lakes, a type of fish occurs which agrees closely with *S. alpinus* of the Gulf of Alaska area, while in streams there occurs a smaller form which is distinct from *S. malma* south of the Alaska Peninsula. This stream-dwelling form is here regarded as a northern form of *S. malma*.

From the data presented, *S. alpinus* and *S. malma* are considered as discrete species, each subject to geographic variation, which occur sympatrically in certain areas of Alaska (Fig. 3) with little or no hybridization.

In the following sections each species will be treated separately. The species will be described, its distribution discussed, and the validity of its subspecies examined.

DESCRIPTION OF *SALVELINUS MALMA*

The following description includes data from the entire North American range of *S. malma*. Where there are distinct forms of *S. malma* the differences between these forms are noted.

Head 3.2 to 5.8 into fork length (Fig. 4). D. 13–16 (all rays); A. 11–15 (all rays). Body elongate, somewhat rounded; vertical eye diameter 4–5.5 into head; mouth terminal, large; maxillary usually reaching to a point behind posterior margin of the eye. In dwarf stream-dwelling forms the maxillary often does not reach beyond the posterior margin of the eye. Teeth

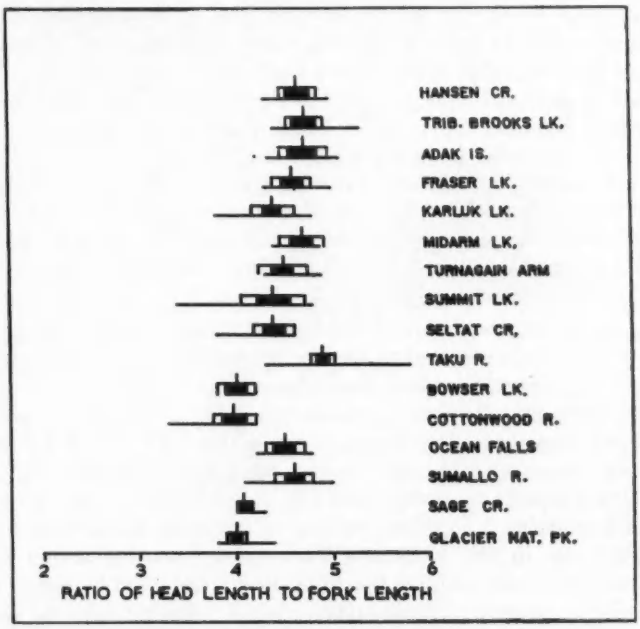

FIG. 4. Geographic variation in the ratio of head length to fork length for North American *S. malma*.

FIG. 3. North American distribution of *S. malma* and *S. alpinus*.

on head of vomer only, palatine teeth and vomerine teeth sometimes continuous, usually not; 7–15 teeth on tongue; 0–44 teeth on the basibranchial bones, the number of teeth on the basibranchial bones increases with length. Gill rakers on first arch 11–26; gill rakers on lower limb of first arch 8–14 (11–14 in the northern form, 8–12 in the other forms); gill rakers on upper limb of first arch 3–9. Pyloric caeca 13–47 (19–47 in the northern and southern forms, 13–18 in the central Alaska form). Branchiostegal rays 21–30, usually more on left side than on right side. Total number of vertebrae 57–70 (65–71 in the northern form, 57–66 in the other forms). Lateral line slightly decurved anteriorly, then straight, often with a dip or arch posteriorly; pores along the lateral line 105–142.

Colour variable; blue, olive-green or brown on dorsal surface; occasionally bright red on sides, sea-run individuals silvery. Pelvic and anal fins often with creamy leading edges. Some individuals with a distinct dark streak along the inner edge of the dentary. Yellow, orange or red spots on dorsal surface and sides; spots round, small and numerous, the largest touching lateral line 3–7 times into interorbital width. Dorsal surface occasionally with vermiculations. Juveniles and dwarf adults with 8–10 wide parr marks.

Distribution

Salvelinus malma ranges from northern California around the rim of the North Pacific and Bering Sea to Japan and Korea (Fig. 3). Over most of this range *S. malma* has both anadromous and non-migratory populations. At the southern extremes of its range *S. malma* is usually non-migratory. Taranetz (1936) reports anadromous populations of *S. malma* as far south as Peter the Great Bay. Non-migratory forms are found in southern Honshu and in the Yalu River (Taranetz, 1936). In North America (Fig. 5) the southern extent of the range is represented by isolated, non-migratory populations in northern Nevada (Miller and Morton, 1952) and northern California (Wales, 1957).

In Asia *S. malma* is reported north to the Anadyr River (Berg, 1948). The exact northern limits of the range in North America are unknown. *Salvelinus malma* has been reported from Point Hope and Herschel Island (Scofield, 1899), and from the Colville River mouth, Perguiak and Point Barrow on the arctic slope of Alaska (Murdoch, 1885). However, *S. alpinus* is common in these areas, and some records of *S. malma* may be due to confusing the two species. Figure 3 gives the northern range of *S. malma* in North America based on specimens examined by the author.

S. malma is not common in central Alaska and central Yukon Territory, where it appears to be confined to head-water habitats. Evermann and Goldsbourough (1907) report *S. malma* from Mynock Creek (tributary to the Yukon River) near Rampart. The only *S. malma* obtained by the present author from central Alaska were from Dry Creek, a small tributary of the Tanana River. No *S. malma* were taken in the Tanana or Yukon Rivers proper. Wynne-Edwards (1947) reports *S. malma* from the clear streams of the Mackenzie and Richardson Mountains. *Salvelinus alpinus* occurs in the Richardson Mountains, and probably also in the Mackenzie Mountains. Lacking actual specimens, Wynne-Edwards' records of *S. malma* from these areas could be due to confusing *S. malma* with *S. alpinus*. Preble (1908) reports *S. malma* from the headwaters of the Peel River. Some of the headwaters of the Peel rise in the Mackenzie Mountains, and Preble's record also should be treated with reservation. *S. malma*

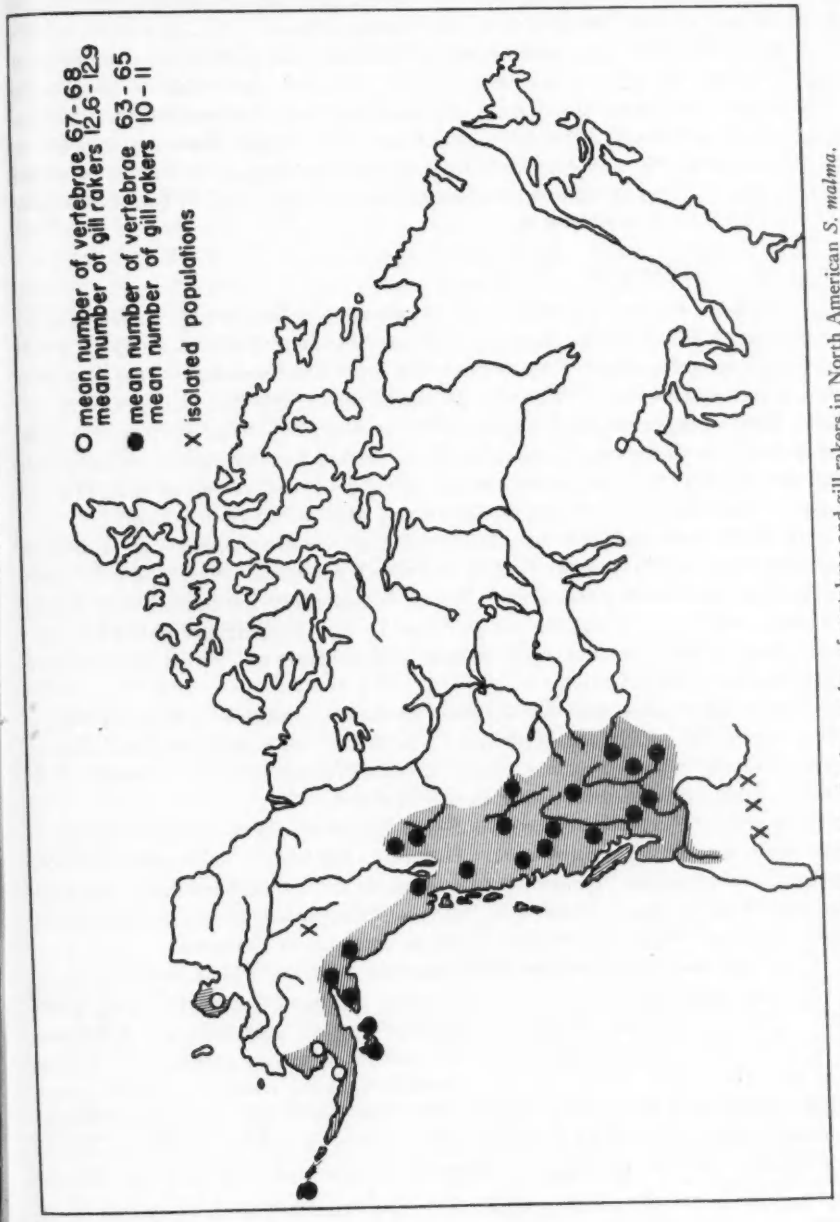
O mean number of vertebrae 67-68
mean number of gill rakers 12.6-12.9
● mean number of vertebrae 63-65
mean number of gill rakers 10-11
X isolated populations

FIG. 5. Geographic variation in the number of vertebrae and gill rakers in North American *S. malma*.

is widely distributed in the upper Liard River (Mackenzie system), and in the Swift River, a small headwater of the Yukon River.

In British Columbia *S. malma* is widely distributed in all river systems except the Okanagan (Carl and Clemens, 1953). On the east slope of the Rocky Mountains *S. malma* is abundant in the headwaters of the South Saskatchewan, North Saskatchewan, Athabaska and Peace Rivers but does not extend far onto the plains. *S. malma* is widely distributed throughout most of the Columbia River system, but has only been reported once (Hubbs and Miller, 1948) from the Snake River above Shoshone Falls.

Validity of Subspecies

Salvelinus malma was originally described from the rivers of Kamchatka (Walbaum, 1792). Recent Russian authors (Taranetz 1933, 1936; Berg, 1948) recognize two subspecies[6], *S. m. malma* and *S. m. krasheninnikovi* Taranetz from the Pacific coast of Asia. *S. m. malma* is distributed north of the Gulf of Amur, while *S. m. krasheninnikovi* is distributed south of the Gulf of Amur. *S. m. krasheninnikovi* is distinguished from *S. m. malma* by the number of vertebrae and the number of pores along the lateral line (59–64 vertebrae and 115–133 pores in *krasheninnikovi*, 64–69 vertebrae and 132–140 pores in *malma*).

In North America there are also two distinct forms of *S. malma*. The form found north of the Alaska Peninsula has 65–71 vertebrae and 11–14 gill rakers on the lower limb of the first arch. The *S. malma* occurring south of the Alaska Peninsula and in the Aleutian Islands have 57–67 vertebrae and 8–12 gill rakers on the lower limb of the first arch. There is no evidence of a broad cline between these two forms (Fig. 5).

The northern and southern forms of *S. malma* probably originated from a single population which was divided by glaciation. The northern form evolved in the unglaciated coastal areas of Alaska and Siberia. In North America the southern form evolved to the south of the ice sheet.

In number of vertebrae the two North American forms are in close agreement with the Russian subspecies. However, the exact relationship between the North American and Asiatic forms can not be determined until more information becomes available. Until such a time it is convenient simply to refer to the North American forms of *S. malma* as either northern or southern.

Four specimens of *S. malma* were obtained from Dry Creek near Fairbanks in the unglaciated portion of central Alaska. Comparison of the Dry Creek Dolly Varden with other populations revealed a major morphological difference. The Dry Creek specimens had a very low number of pyloric caeca, ranging from 13 to 18 with a mean of 16. In normal populations the number of pyloric caeca ranges from 19 to 47 with a mean of 26 to 28. The Dry Creek population probably represents a distinct form of *S. malma* which has been isolated in central Alaska since before the last glaciation. Whether the central Alaska Dolly Varden

[6]Taranetz (1936) lists two infraspecies from Russia, *Salvelinus malma* infraspecies *curilus* (Pallas) and *Salvelinus malma* infraspecies *kuznetzovi* Taranetz. These forms are apparently ecotypes.

warrant subspecific designation cannot be determined until more specimens become available.

Jordan *et al.* (1930) suggest that in North America *S. malma* intergrades southwards to form the subspecies *Salvelinus malma spectabilis*. *S. m. malma* is said to be distinguished from *S. m. spectabilis* by the length of the head (less than $\frac{1}{4}$ into standard length in *S. m. malma*, more than $\frac{1}{4}$ in *S. m. spectabilis*). Figure 4 indicates that there is some geographic variability in the length of the head relative to body length, but no evidence to support subspecific distinction based on this character.

Jordan *et al.* (1930) list the Japanese *Salvelinus pluvius* (Hilgendorf) as a synonym of *S. malma*. Recent Japanese authors (Aoyagi, 1957; Matsubara, 1955; Okado, 1955) consider *S. pluvius* to be a distinct species. Aoyagi (1957) distinguishes *S. malma* from *S. pluvius* on the basis of gill rakers and parr marks (16-26 gill rakers and no parr marks in adult *S. malma*, 11–20 gill rakers and parr marks in adult *S. pluvius*). The gill raker count for *S. pluvius* is based on 7 specimens. Even with this small number the gill raker count considerably overlaps that given for *S. malma*. In North America stunted populations of *S. malma* commonly have parr marks as adults. Aoyagi (1957) reports *S. malma* from Hokkaido and *S. pluvius* from Honshu; presumably their ranges never overlap. The evidence suggests *S. pluvius* is a geographic form of *S. malma* and probably should not be considered a distinct species. Whether *S. pluvius* should be considered a separate subspecies of *S. malma* cannot be determined from the available evidence.

Bailey *et al.* (1954) suggest that "a species is properly divisible into subspecies when data have been suitably published to demonstrate that it consists of two or more allopatric populations, each displaying a high degree of uniformity over its range and differing with a high constancy (a figure of at least 93 per cent of individuals is suggested) from other forms, each of which intergrades over a relatively narrow geographic area with at least one other form". In North America there are at least two allopatric forms of *S. malma* which probably fulfill the above criteria. However, in order to avoid synonymies these forms should not be given subspecific designation until their relationship to Asiatic subspecies can be determined.

DESCRIPTION OF *SALVELINUS ALPINUS*

The following description includes data from the entire North American range of *S. alpinus*. Where there are distinct forms of *S. alpinus* the differences between these forms are noted.

Head 3.6–4.8 into fork length. D. 12–16 (all rays); A. 11–15 (all rays). Body elongate, somewhat rounded; vertical eye diameter 3.8–5.4 into head; mouth terminal, large; maxillary usually reaching past posterior margin of the eye. In non-migratory populations the maxillary often does not reach beyond the posterior margin of the eye. Teeth on head of vomer only; spacing between the palatine and vomerine teeth variable; 10–24 teeth on tongue; 20–85 teeth on the basibranchial bones (the number of teeth on the basibranchial bones is extremely variable within populations). Gill rakers on lower limb of first arch 12–19 (mean in the lower Yukon

area approximately 13.5, mean over the rest of the North American range approximately 16); gill rakers on upper limb of first arch 7–13. Pyloric caeca 20–74 (mean in lower Yukon area approximately 29, mean over the rest of the North American range is usually near 44). Total number of vertebrae 60–71. Lateral line slightly decurved anteriorly, then straight, often with a dip or arch posteriorly; pores along the lateral line 123–152.

Colour variable; blue, olive green or brown on dorsal surface; sides often bright orange or red, sea-run individuals silvery. Pelvic and anal fins often with creamy leading edges. Usually a distinct dark streak along the inner edge of the dentary. Pale pink to red spots on dorsal surface and sides (some individuals without spots); spots round, those along the lateral line are usually semi-circular; spots less numerous than in *S. malma* and usually larger, 1.8–6 times into interorbital width. In the Bering Sea region the spots above the lateral line often have a narrow blue halo. Juveniles and dwarf adults with 8–15 wide parr marks.

Distribution in North America

S. alpinus is circumpolar in distribution. In North America it ranges from Alaska along the Arctic coast to the New England states (Fig. 6). Over most of this range *S. alpinus* has both anadromous and non-migratory populations, but at the southern extremes of its range it is usually non-migratory. In North America the southern limit is represented by non-migratory populations on Kodiak Island in the west and by isolated, non-migratory populations in Quebec, Newfoundland, New Brunswick, New Hampshire and Maine in the east. *S. alpinus* extends northward to the limit of land.

In Hudson Bay *S. alpinus* is distributed south to the Churchill River (Vladykov, 1933) on the west coast of the bay, and to Cape Jones on the east coast (Halkett, 1919).

In the Northwest Territories *S. alpinus* is widely distributed along the sea coast. Anadromous *S. alpinus* ascend most of the rivers. *S. alpinus* ascends the Thelon River as far as Beverly Lake, and is distributed throughout the Back River system. *S. alpinus* ascends the Mackenzie River as far as Ft. Good Hope (Wynn-Edwards, 1947). Wynne-Edwards also reports chars from the Mackenzie and Richardson Mountains; it is not known whether these are *S. malma* or *S. alpinus*.

S. alpinus is widely distributed along the Arctic and Bering Sea coasts of Alaska. Anadromous populations ascend most rivers. Walters (1955) reports *alpinus*-like chars from the headwaters of the Colville, Hulahula and Yukon Rivers. The species of these chars is not known. In the lower Yukon and Kuskokwim area *S. alpinus* is found mainly in clear lakes and streams.

Validity of Subspecies

Salvelinus alpinus was originally described from Scandinavia. At present the taxonomy of the European chars is confused. As a result it is not possible to determine the relationship of North American to European *S. alpinus*.

The following species of Arctic chars have been described from the eastern Canadian arctic; *Salvelinus rossii* (Richardson), *Salvelinus alipes* (Richardson), *Salvelinus nitidus* (Richardson), *Salvelinus arcturus* (Günther) and *Salvelinus*

O mean number of gill rakers 13-14
mean number of pyloric caeca 27-31
● mean number of gill rakers 15-17
mean number of pyloric caeca 36-53
X isolated populations

FIG. 6. Geographic variation in the number of gill rakers and pyloric caeca in North American *S. alpinus*.

naresii (Günther). These species were based on small samples and were inadequately described. Where the descriptions mention gill rakers, pyloric caeca or vertebrae the number is always within the range for *S. alpinus*. Examination of anadromous and non-migratory chars from Alaska, Northwest Territories and Labrador revealed no evidence to support the division of the North American Arctic chars into several species.

S. alpinus is represented in Quebec, New Brunswick, Newfoundland, New Hampshire and Maine by isolated, non-migratory populations. These populations were originally given specific designation: *S. marstoni* (Garman) in Quebec, *S. aureolus* (Bean) in New Hampshire and Maine, and *S. oquassa* (Girard) in western Maine. Backus (1957) considers these forms glacial relicts of *S. alpinus*. Vladykov (1954) suggests that *S. marstoni* and *S. oquassa* may be the same species, but that *S. aureolus* is a distinct species. Vladykov (1957) has divided *S. marstoni* into three subspecies: *S. marstoni marstoni*, *S. marstoni intermedius* and *S. marstoni cavanaghi*. These subspecies are largely based on characters that Vladykov (1954) dismissed as being useless in char taxonomy.

In number of gill rakers, pyloric caeca and vertebrae *S. marstoni*, *S. aureolus* and *S. oquassa* are all within the range of variation for North American *S. alpinus*. Vladykov (1954) has suggested that the details of the caudal skeleton are useful in distinguishing *S. alpinus*, *S. marstoni* and *S. aureolus*. Examination of radiographs of 70 specimens of *S. alpinus* and *S. malma* reveal that the range of variation in the details of the caudal skeleton is very wide. Such characters are evidently of little value in distinguishing closely related species of chars. For these reasons *S. marstoni*, *S. aureolus* and *S. oquassa* are considered synonyms of *S. alpinus*. Whether these forms warrant subspecific status can not be determined on the available evidence.

In western North America there are two distinct forms of *S. alpinus* (Fig. 6). The *S. alpinus* distributed from the lower Kuskokwim to the Mackenzie River have 20–36 pyloric caeca (with a mean of approximately 29) and 12–15 gill rakers on the lower limb of the first arch (with a mean of approximately 13.5). The *S. alpinus* distributed east of the Mackenzie River, and those south of the Kuskokwim, have 25–74 pyloric caeca (with a mean of approximately 44) and 12–17 gill rakers on the lower limb of the first arch (with a mean of approximately 16).

Figure 6 suggests that the eastern form of *S. alpinus* (black dots) was once continuously distributed across the North American arctic. It is suggested that this continuous distribution was interrupted by a glaciation (perhaps the Wisconsin). Populations of this form probably survived in the Bristol Bay area, and perhaps on Kodiak Island, as well as south of the ice sheet in eastern North America. The form represented by the white dots in Fig. 6 probably evolved along the arctic slope of Alaska and Siberia. The forms were geographically isolated by the Bering land-bridge in the west and the Continental ice-sheet in the east. The present distribution of both forms has probably been attained by post-glacial dispersal from the above mentioned areas.

These forms of *S. alpinus* may warrant subspecific designation. However, this should be avoided until the relationship between the Eurasian and North American forms of *S. alpinus* can be determined.

ORIGIN AND DISPERSION OF *S. MALMA* AND *S. ALPINUS*

The morphological similarity between *S. malma* and *S. alpinus* suggests that they are derived from a common ancestor. Some speculation can be made concerning the time at which *S. malma* and *S. alpinus* diverged.

Ekman (1953) presents evidence indicating a fairly comprehensive faunistic connection between the cold-temperate faunas of the Atlantic and Pacific during the late Pliocene or early Pleistocene. If *S. malma* had been differentiated at this time it is likely that it would have reached the North Atlantic. Relict populations of *S. malma* in unglaciated parts of Alaska, northern California, Japan and Korea indicate that *S. malma* was widely distributed in the North Pacific area prior to the last Pleistocene glaciation. Relict populations of *S. alpinus* in Quebec, New Brunswick, Newfoundland, New Hampshire, Maine and Europe indicate that *S. alpinus* was widely distributed in the North Atlantic area prior to the last Pleistocene glaciation. *S. malma* and *S. alpinus* must, therefore, have diverged sometime in the Pleistocene prior to the last glaciation.

Before the first Pleistocene emergence of the Bering land-bridge the ancestor of *S. malma* and *S. alpinus* was probably distributed continuously from the North Pacific to the North Atlantic. During the Pleistocene the North Pacific was separated from the Arctic Ocean several times by the land-bridge. During one of these periods of isolation *S. malma* probably evolved to the south of the land-bridge and *S. alpinus* to the north. It is generally accepted that the land-bridge was flooded during the interglacial periods, although Ekman (1953) indicates that very little is known about possible interglacial communications between the North Pacific and North Atlantic. *S. malma* must have evolved prior to one of these interglacial floodings, but did not extend itself into the Atlantic. Neave (1958) suggests that throughout the available interglacial intervals the physical conditions of the Polar Sea did not become much more favourable than they are at present. The present range of *S. malma* does not extend far, if at all, into the Arctic Ocean. It may be supposed that there is some physical factor limiting the northward distribution of *S. malma* and that this prevented the spread of *S. malma* into the Arctic Ocean during the interglacial periods. *S. alpinus* probably reinvaded the North Pacific during each interglacial period.

Morphologically *S. malma* and *S. alpinus* are very similar. Both species spawn in the fall or early winter. Evidence from related species (Stenton, 1952; Buss and Wright, 1956) suggest that the interbreeding of *S. malma* and *S. alpinus* would produce fertile offspring. Therefore, some mechanism for preventing hybridization must have evolved while *S. malma* and *S. alpinus* were geographically isolated. It is suggested that the incipient species developed differences in spawning behaviour which prevented interbreeding after the geographical barriers separating them were broken down. This suggestion is

supported by the spawning behaviour of the two species in Karluk Lake. In the Karluk system *S. malma* spawns in tributary streams, and *S. alpinus* spawns in lakes (DeLacy and Morton, 1942). This behavioural difference, where absolute, could provide a mechanism which prevents formation of hybrids.

In North America *S. malma* probably survived the last Pleistocene glaciation in two areas. Morphologically distinct populations in the unglaciated areas of Alaska suggest that *S. malma* survived in that area. The present range of *S. malma* extends well south of the southern limits of glaciation and suggests that *S. malma* also survived south of the ice sheet on the west side of the continental divide. The present North American distribution of *S. malma* has probably been attained by both freshwater and marine dispersion mainly from south of the ice sheet. *Salvelinus malma* is often found in headwater streams which are highly susceptible to piracy from other watersheds. Possibly *S. malma* reached the east slope of the Rocky Mountains by this means. The anadromous habit accounts for the wide coastal distribution of *S. malma*.

In North America *S. alpinus* probably survived the last Pleistocene glaciation in the unglaciated areas of Alaska, and south of the ice sheet in eastern North America. The present North American distribution of *S. alpinus* has probably been attained largely through marine dispersion from these centres.

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APPENDIX

A summary of the meristic data on which this study is based. The localities are arranged in a south-north order. The latitudes and longitudes are approximate.

Locality	N Lat.	W Long.	Number of specimens	Gill rakers Range	Gill rakers Mean	Vertebrae Range	Vertebrae Mean	Pyloric caeca Range	Pyloric caeca Mean	Pores along lateral line Range	Pores along lateral line Mean
S. malma—SOUTHERN FORM											
Gilfer Cr.	48° 30′	114° 05′	3	5–6+11–12	5+11	...	...	25–30	27.6	124–133	128.1
Logging Cr.	48° 30′	114° 10′	2	3–5+11–12	4+11	60–66	63.2	31–37	34	129–131	130
Fish Cr.	48° 30′	114° 10′	2	4–6+10–11	5+11	...	...	26–27	26.5	127–132	128.8
Sage Cr.	49° 10′	115° 07′	15	5–7+10–12	6+11	62–66	64	26–34	30	114–138	125.2
Sumallo R.	49° 17′	121° 14′	30	6–8+10–12	7+10	62–66	64.9	20–32	24.1	114–138	128.3
Pitt L.	49° 20′	122° 35′	6	4–8+11–12	6+11	...	...	19–24	22.1	126–131	128.9
Chehalis L.	49° 25′	122° 02′	17	4–8+10–12	6+11	...	...	22–32	24	120–135	127
Homathko R.	51° 00′	124° 55′	4	6+10–11	6+10	...	...	23–32	28.7	...	...
Cuthead L.	51° 10′	115° 45′	20	4–7+10–11	6+10	60–66	63.8	21–33	26.2	114–142	129.1
Adak I.	52° 00′	176° 40′	30	5–9+10–12	6+11	60–65	64.4	20–31	27.6	112–142	127
Ocean Falls	52° 40′	127° 35′	36	5–8+9–11	6+10	59–65	64.3	19–32	24.2	105–140	126.8
Cottonwood R.	53° 00′	122° 32′	15	4–6+10–12	5+11	58–66	63.4	23–32	28	123–137	130
Peace R.	56° 08′	121° 05′	5	5–7+10–12	6+11	62–65	63.9	23–32	27.1	121–140	132
Bowser L.	56° 30′	129° 30′	9	5–6+10–11	5+11	57–66	63.3	22–32	29	126–137	130
Fraser L.	57° 15′	154° 09′	38	4–8+8–12	5+10	62–66	64	26–47	35.4	117–140	127
Karluk L.	57° 23′	154° 05′	33	4–8+8–12	7+11	62–66	64	24–34	28.1	111–133	124
Midarm L.	58° 11′	152° 25′	30	6–8+11–12	7+11	58–66	64.1	25–36	27.8	115–138	123
Taku R.	58° 32′	133° 52′	25	5–8+10–12	7+10	60–66	64.2	21–31	27	115–141	130
Saltat Cr.	59° 36′	136° 29′	30	6–8+9–12	7+10	59–65	63	19–40	25.8	113–141	128.3
Kelsall L.	59° 48′	136° 32′	3	7–8+9–11	7+10	61–65	63	21–27	24.9	122–139	128
Swan L.	59° 53′	131° 24′	2	5–6+11	5.5+11	64	64	31–33	32	131–134	132.5
Little L.	60° 00′	130° 30′	4	5–7+10–12	6+11	64–66	65	23–26	25.2	103–125	118
Partridge Cr.	60° 00′	131° 50′	6	5–7+9–11	5+11	64–66	65.1	26–33	27.8	105–130	120
Kenai R.	60° 28′	151° 24′	1	...	8+12	...	65	...	27	...	128
Upper Trail L.	60° 31′	149° 24′	2	7–8+12	7.5+12	...	65	27–28	27.5	118–127	122.5
Summit L.	60° 37′	149° 31′	30	5–8+10–12	7+11	60–66	64.2	22–46	31	116–139	129
Turnagain Arm	60° 57′	149° 21′	20	5–8+9–12	7+10	57–66	64.1	16–27	20.2	110–135	124.2
Chena L.	61° 32′	144° 26′	5	8+10–12	8+11	59–65	64.1	21–26	24	129–143	135
S. malma—NORTHERN FORM											
Brooks L.	58° 22′	156° 00′	20	7–10+11–14	9+12.6	67–69	68	21–36	27.9	106–142	132.6
Hansen Cr.	59° 12′	158° 35′	30	8–10+11–14	9+12.9	66–70	67.6	21–30	26.7	111–140	128.7
Salmon L.	64° 50′	165° 00′	30	7–10+11–14	9+12.8	65–71	67.8	24–31	28	115–141	127
S. malma—DRY CREEK											
Dry Cr.	63° 41′	144° 00′	4	7–9+10–11	7+11	62–64	63	13–18	16	130–138	134

APPENDIX (continued)

S. alpinus—EASTERN ARCTIC											
Flaherty I.	55° 59′	79° 00′	10	9–13+14–17	11+16	...	...	30–52	44.7	...	...
Nain	56° 32′	61° 40′	3	9–11+15–16	10+15.7	...	...	40–44	42.6	...	...
Ft. Chimo	58° 15′	68° 05′	1	...	10+16	...	...	...	...	...	...
Merewether Crat.	61° 13′	73° 40′	10	9–12+15–17	11+16	64–67	66	31–47	36.9	123–152	139.4
Term Pt.	61° 51′	93° 00′	15	9–12+14–17	11+15.7	...	...	30–46	41	123–140	136
"Shona" L.	63° 30′	68° 50′	10	8–10+14–17	9+16	...	...	34–48	43.7	...	...
Armit L.	64° 06′	91° 32′	15	9–12+15–17	11+16	...	...	35–48	44	126–147	136
Sapuladjuk	64° 18′	76° 30′	10	9–12+14–17	10+16	...	...	35–47	42	...	...
Beverly L.	64° 35′	100° 38′	1	...	10+16	...	...	...	44	...	140
Beechey L.	65° 12′	106° 28′	2	10–13+16–17	11.5+16	...	...	40–46	43	...	141
MacDougal L.	65° 59′	98° 34′	2	11–12+17–18	11.5+17.5	...	...	45–47	46	136–146	141
Kathawachaga L.	66° 11′	111° 08′	16	9–12+16–19	11+18	65–68	67	38–58	45	127–149	138.1
Nettilling L.	66° 18′	70° 40′	8	9–12+15–16	11+15.7	...	...	29–46	39	137–150	140.3
Bloody Falls	67° 59′	115° 30′	10	9–12+13–16	11+15	...	...	26–51	46	130–142	136.9
Bernard Hb.	68° 48′	116° 10′	11	10–13+14–17	12+15.4	...	...	36–53	45	...	...
King William I.	69° 00′	98° 10′	1	...	10+16	...	69	...	46	...	144
Pond Inlet	70° 31′	77° 25′	1	...	12+17	...	66	...	...	...	...
Resolute Bay	74° 43′	94° 20′	6	9–11+14–17	10+16	...	...	36–47	41	...	...
Devon I.	76° 00′	86° 00′	2	9–11+15	10+15	...	...	42–47	44.5	...	...
Mould Bay	76° 12′	119° 09′	7	10–13+16–18	11+16.7	...	...	41–46	44	...	...
South Fiord	79° 24′	91° 55′	4	+15–18	+16	Data courtesy K. E. Ricker			...	...	...
Victoria L.	81° 49′	70° 30′	1	...	12+16	...	67	...	38	...	131
S. alpinus—BERING SEA AND WESTERN ARCTIC											
Nunivak I.	60° 00′	167° 00′	2	8–10+13–14	9+13.5	...	68	30–31	31.5	126–143	134.5
St. Matthews I.	61° 20′	172° 30′	10	8–11+12–14	9+13	...	...	28–44	30	...	...
Aniak R.	61° 35′	159° 40′	7	8–10+12–15	9+13	66–67	66.5	24–31	27	...	...
Tolstoi L.	63° 10′	157° 45′	30	7–10+12–15	9+13.7	...	...	23–32	27.8	...	...
St. Lawrence I.	63° 17′	169° 00′	40	7–11+12–14	9+13	...	...	21–35	28	135–147	138
Unalakleet R.	63° 52′	160° 55′	2	10+13–14	10+13.5	...	...	23–33	28	...	...
Nome R.	64° 28′	165° 20′	1	...	9+12	...	...	...	24	...	...
Nulato R.	64° 40′	158° 05′	3	9–10+13–14	9+13.3	...	...	20–27	23	135–140	138
Pt. Clarence	65° 10′	166° 30′	1	...	9+13	...	...	...	...	...	...
Pt. Hope	68° 20′	167° 00′	2	...	9+13	...	...	...	...	...	...
Aklavik	68° 20′	134° 30′	1	...	10+13	...	...	...	35	...	...
Chandler R.	69° 27′	151° 25′	1	...	10+14	...	...	...	...	...	...
Collison Pt.	69° 35′	139° 07′	2	11+12–13	11+12.5	...	...	28–31	29.5	...	140
Herschel I.	69° 35′	139° 00′	3	10+12–14	10+13	...	...	29–35	32.3	138–144	140
Oliktok Pt.	70° 30′	149° 50′	1	...	10+14	...	...	...	...	...	...
Elson Lagoon	71° 15′	156° 10′	3	...	9+13	...	...	28–30	29	...	...
S. alpinus—BRISTOL BAY AND GULF OF ALASKA											
Fraser L.	57° 15′	154° 10′	54	8–11+12–16	9+15	65–69	67	36–55	42.9	127–153	140.2
Karluk L.	57° 23′	154° 09′	32	8–11+12–16	9+14.6	65–69	67	35–57	44.3	120–155	134.4
Brooks L.	58° 22′	156° 00′	1	...	11+14	...	...	...	43	...	140
Aleknagik L.	59° 15′	158° 35′	30	8–10+12–17	9+15.1	66–71	67.6	29–74	52.5	...	...
Nerka L.	59° 25′	159° 00′	30	8–10+13–16	9+15.5	66–71	67.6	37–64	49	126–150	141
Idavain L.	59° 15′	156° 00′	1	8–10+14–16	9+14.7	...	...	...	...	...	...

Detection of Incomplete Reporting of Tags[1,2]

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ABSTRACT

A table is presented which gives the total number of tags that must be recovered in order to have a prescribed probability of discovering non-reporting by fishermen of a certain percentage of recaptured tags when a portion of the catch or of the effort is inspected by special observers. The table gives the required sample sizes for probabilities of detection of 0.50, 0.80, 0.90, 0.95, and 0.99 at various levels of catch inspection. The table may also be used to find the sample size needed to detect with prescribed probability a differential mortality between two identifiable groups of fish whose initial numbers are known. A number of examples of the use of the table are included.

INTRODUCTION

When the primary objective of a tagging or marking experiment is to estimate the rate of exploitation of a population supporting a fishery, it almost invariably follows that the actual recovery of the bulk of the tagged or marked fish is out of the hands of the investigators conducting the experiment. A major part of the responsibility of detecting and reporting recaptures of tagged fish must be entrusted to the commercial, sport or native fishermen who harvest the population.

Attempts to enlist the cooperation of the fishermen and to increase their effectiveness in recovering tags have ranged from educational programs to various reward schemes. Measures aimed at overcoming possible disinterest on the part of the fishermen and increasing their incentive to search for and to turn in tags have been particularly imaginative. For example, for returning a tag to the Inter-American Tropical Tuna Commission, the fisherman receives $1 and a chance in an annual $300 drawing (Schaefer, 1958). The Fisheries Research Institute at the University of Washington has approached the motivation problem in a forthright manner by proffering a reward of $25 for the return of both fish and attached tag for recoveries of tagged salmon released in the North Pacific; this was accompanied by 2-fold increase in the percentage of tags returned (personal communication from Allan Hartt). To attribute this increase solely to the change in the value of the reward (from $5 to $25) is an oversimplification of a highly complex problem but the magnitude of the increase does lead to interesting speculation.

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Recovery programs that depend on voluntary tag reporting by sports fishermen appear to be subject to particularly high levels of non-response error. Angler response also appears to be highly sensitive to a variety of factors and is apt to fluctuate markedly depending on the accompanying circumstances, e.g., in one of two studies conducted in Massachusetts, Mullan (1959) found a 60% non-response for mandible tags on trout; and in the other, Stroud and Bitze (1955) estimated a 25% non-response for strap and cheek tags on warm-water species. A recent article by McCammon and LaFaunce (1961) should be consulted for a more complete discussion of the incomplete reporting problem for freshwater sport fisheries.

While rewards and other such measures decrease the possibility of non-reporting of tags, each tagging experiment should be so designed as to contain some provisions for testing the assumption that all of the recaptured tags are turned in. The most direct method of testing this assumption is to have trained observers examine a portion of the catch. A sampling program of this sort may be objectionable because of the manpower requirements and because of the cost involved but it would seem to be unavoidable except in special circumstances.

The purpose of this note is to provide the biologist planning a tagging experiment with a preliminary guide to help him decide how many tags should be put out and how much of the catch should be inspected to be reasonably sure of discovering non-reporting of a certain magnitude. When the total outlay for the tagging experiment is fixed the table furnished here should also be an aid in allocating personnel and resources to best advantage between the tagging and recovery phases of the experiment. There may be a temptation to sample the catch for marks in a perfunctory manner and to conclude that incomplete reporting is not a serious problem unless a sizeable difference between the tagged to untagged ratios for the inspected and uninspected portions of the catch shows up. Table I shows that if only "token" catch sampling is carried on, there is a rather large chance that a significant amount of incomplete reporting will not be detected. Or, to view the problem in a slightly different perspective, if we wish to maintain the same assurance of detecting incomplete reporting, a substantial increase in the numbers of fish tagged may be required to offset a decrease in the proportion of the catch inspected.

THEORY AND METHODS

If incomplete reporting is extensive, the apparent rate of exploitation or the apparent size of the population as calculated from the tag returns may be seriously biased. The true rate of exploitation is equal to the apparent rate divided by the fraction of tags that are reported (Ricker, 1958). A convenient term for this fraction is the *reported ratio* which has been defined as (to paraphrase Atwood and Geis, 1960): the fraction of the total number of tagged or marked fish caught that are subsequently reported to the research agency.

In the development that follows it is assumed that the reported ratio remains constant throughout the experiment and over the entire area in which the

recoveries are made. If these conditions are not met, it may be possible to subdivide the recoveries into groups so that the reported ratio for each sub-division is constant.

The need for such stratification should obviously be explored if the recoveries are made by nationals of several countries in an internationally fished area (Beverton and Holt, 1957, p. 200), or the publicity given to the experiment is unevenly distributed over the exploited area. A time stratification might be called for if there is reason to suspect a tag may be retained by the fishermen as a talisman when it is first introduced (Idyll, 1952; Rounsefell and Everhart, 1953). A number of specific examples of areal and temporal variations in the reported ratios for banded waterfowl are presented by Atwood and Geis (1960).

A natural formulation of the problem of detecting incomplete reporting is as a test of the hypothesis that the reported ratio is equal to 1, against the alternative that the reported ratio is less than 1. The probability of detecting a reported ratio that is less than 1 with such a test (this probability is generally referred to as the "power" of the test) will be examined using the following notation:

- ρ reported ratio (tags reported ÷ tags captured)
- f_i number of standardized units of gear in the ith class ($i = 1,2$)
- C_i catch in numbers in the ith class
- r_i number of tags recovered in the ith class ($r = r_1 + r_2$)
- s_i number of tags reported from the ith class ($s = s_1 + s_2$)
- t number of tags liberated
- N number of fish in population at time of tagging
- Z standardized normal variate, $\Pr(Z \geq z_{1-\alpha}) = \alpha$
- α level of significance of the test, or the probability of rejecting the null hypothesis when true, i.e., concluding that $\rho < 1$ when in fact $\rho = 1$
- β probability of concluding that ρ is equal to 1 when in fact ρ is less than 1

More adequate definitions of the statistical terms may be found in any standard text on statistics, e.g., see Chapter 7 of Dixon and Massey (1957).

Observe that α and β are the respective probabilities of two opposite types of error:

- α is the probability of erroneously concluding that some tags are not reported when in fact all are reported.
- β is the probability of failing to detect that some tags are not reported when in fact only the fraction ρ of them is reported.

It is necessary to specify acceptable levels for both of these in order to compute the number of fish that should be marked.

The procedure outlined below presupposes the feasibility of classifying either the catch or fishing effort into two categories, one of which has a known reported ratio of unity or nearly so, while the other has an unknown reported ratio that is to be estimated from the tag recoveries. In practice, the former category would

be defined as the fraction of the catch or the effort inspected by special observers; or, possibly, as the units of gear operated by fishermen who, by virtue of special training, long experience, or a keen interest in the experiment, could be relied upon to turn in all of the tags that appear in their catches. The sampling for tags might easily be coordinated with the collection of other biological data. For example, the International Pacific Halibut Commission at present assigns a biologist to each of a number of the vessels in the halibut fleet. One of the biologist's routine duties is to inspect the catch as it is brought aboard (personal communication from R. J. Myhre).

CATCH SAMPLING

A simple probability model may be formulated in terms of catch inspection. For most commercial fisheries large catches (C_i's) and low tag ratios (t/N's) would be expected. If it is assumed that the same tag ratio applies to both inspected and uninspected classes and that the tag ratio within each class remains constant for the duration of the experiment, the number recovered in each class should be approximately distributed according to a Poisson law (e.g., see Chapman, 1954), i.e.:

$$\Pr(r_i) = \left(\frac{C_i t}{N}\right)^{r_i} \frac{e^{-Ct/N}}{r_i!} \qquad i = 1,2 \tag{1}$$

Now by assumption, $s_1 = r_1$, and it is reasonable to assume further that given r_2, s_2 is binomial (r_2, ρ), i.e.:

$$\Pr(s_2|r_2) = \binom{r_2}{s_2} \rho^{s_2} (1-\rho)^{r_2 - s_2} \tag{2}$$

By a well known result (e.g., see Feller, 1957, p. 269), s_2 is Poisson $\left(C_2 \frac{t}{N} \rho\right)$. It then follows that:

$$\Pr(s_1|s) = \binom{s}{s_1} \left(\frac{C_1}{C_1 + \rho C_2}\right)^{s_1} \left(\frac{\rho C_2}{C_1 + \rho C_2}\right)^{s_2} \tag{3}$$

If the assumption that the tag ratio remains constant during the entire season is permissible, the catch inspection scheme is highly flexible, e.g., all of the fish landed during the first part of the season may be inspected and none of those during the latter part of the season or vice versa. It will be shown below that this assumption may be weakened somewhat provided that catch sampling is carried on in a specified manner. If we assume that the season can be divided into J intervals so that the tag ratio ($= t_j/N_j$ for $j = 1,2, \ldots, J$) remains constant within each interval, then:

$$\Pr(r_{ij}|t_{ij}, N_j) = \frac{e^{-C_{ij} t_j/N_j} \left(\frac{C_{ij} t_j}{N_j}\right)^{r_{ij}}}{r_{ij}!} \tag{4}$$

for $i = 1,2$ and $j = 1,2, \ldots, J$

Under these conditions it is necessary to sample the same fraction of the catch in each of the J intervals. Denoting the constant fraction of the catch inspected by λ it can be easily shown (as above) that:

$$\Pr(s_{1.}|s_{..}) = \binom{s_{..}}{s_{1.}}\left(\frac{\lambda}{\lambda+\rho(1-\lambda)}\right)^{s_1}\left(\frac{\rho(1-\lambda)}{\lambda+\rho(1-\lambda)}\right)^{s_2} \tag{5}$$

where the dot notation is used to indicate summation over a subscript, i.e.:

$$s_{1.} = \sum_{j=1}^{J} s_{1j}$$

Although the Poisson distribution probably applies to most fisheries situations cases may arise, e.g., (when t/N is not small), in which the probability of r_i recoveries may be more adequately approximated by a binomial law, i.e.:

$$\Pr(r_i) = \binom{C_i}{r_i}\left(\frac{t}{N}\right)^{r_i}\left(1-t/N\right)^{C_i-r_i} \tag{6}$$

Equation (6) is equivalent to assuming that two independent random samples of sizes C_1 and C_2 respectively, are drawn from an infinite population for which probability of recovering a tag is t/N. Assuming as before that $s_1 = r_1$ and s_2, given r_2, is binomial (r_2, ρ), we have:

$$\Pr(s_i) = \binom{C_i}{s_i}\left(\frac{\rho_i t}{N}\right)^{s_i}\left(1-\frac{\rho_i t}{N}\right)^{C_i-s_i} \qquad i = 1,2 \tag{7}$$

where $\rho_1 = 1$ and $\rho_2 = \rho$. When the samples taken at all stages are chosen randomly, the exact probability distribution of the recoveries reported by the fishermen could be constructed from the observation that the probability of a total of r recoveries, when a sample of size C is taken, is hypergeometric (Chapman, 1951); given r, C and C_2, the conditional probability of r_2 is again hypergeometric, and the conditional distribution of s_2 given r_2 is binomial (r_2, ρ). Unfortunately, this construction leads to equations that are difficult to manage algebraically.

If the observations are arranged in the usual 2 by 2 table, the chi-square statistic can be used to test the hypothesis H: $\rho = 1$. Since the alternative ($\overline{H}$: $\rho = \rho_a < 1$) is one-sided, we would modify the usual test slightly by only rejecting H when $s_1/C_1 > s_2/C_2$ and the chi-square statistic exceeds $\chi^2_{1-2\alpha}$ instead of the usual $\chi^2_{1-\alpha}$. The limiting power of the chi-square test has been studied by Mitra (1958) and he gives the formulae needed for the power computations and examples of their use. For small numbers of recoveries and small catch sizes the hypothesis that a tag is equally likely to be returned from the uninspected as from the inspected portions of the catch could be tested by Fisher's exact test (Fisher, 1954). Tables and charts of the exact power of this test have been prepared by Bennet and Hsu (1960). Hsu (1960) gives a normal approximation that can be used for power computations when large sample sizes are involved. Another avenue of attack when larger samples are available would be to use the fact that $y_1 = 2 \arcsin \sqrt{s_1/C_1}$ measured in radians has an approximate normal $(2 \arcsin \sqrt{\rho_1 t/N}, 1/C_1)$ distribution. A detailed exposition of the power computa-

tions for the angular transformation and an arcsin table are available in Brownlee (1960).

The present discussion will be restricted to the case where the conditional distribution of the recoveries in a given class can be represented by equation (3). It may be asked what would happen if the Poisson distribution was erroneously assumed when in fact the binomial distribution given in equation (6) did apply. The required sample size as computed from Table I would then be conservative and the true power of the test would exceed the nominal power. A heuristic proof of this statement would be that under the null hypothesis the binomial probability given in equation (3) is replaced by the hypergeometric, i.e.:

$$\Pr(s_1|s) = \frac{\binom{C_1}{s_1}\binom{C_2}{s_2}}{\binom{C}{s}}$$

which has a smaller variance. Since the use of this technique in practice will involve a number of approximations, it is doubtful whether it would be worth the trouble to go through the more exact and more laborious power calculations.

EFFORT SAMPLING

For many fisheries the units of gear are the natural sampling units and effort sampling may actually involve less effort on the part of the research agency. There also may be some advantage in trading the assumptions concerning relations between the tagged and untagged portions of the population which are needed for the catch inspection method for parallel assumptions about the relationship between the tagged population and the fishing effort. Assume that the f_1 units of gear, which have a reported ratio of one, differ in no other way from the other units of gear. Assume further that the fishery is continuous with respect to the tagged populations (see Beverton and Holt, 1957) and that

$$\Pr\begin{pmatrix}\text{tag is recovered by the}\\ \text{research agency between}\\ \text{times } t \text{ and } t + dt\end{pmatrix} = q(f_1 + \rho f_2)e^{-[q(f_1+f_2)+X]t}dt \qquad (8)$$

where X is an instantaneous rate which represents all factors other than the fishery which act to reduce the tagged population and q = ratio of the instantaneous rate of fishing mortality to the fishing intensity. For ρ, f_1, f_2, and X constant, by time $t = T$, a given tag will either have been recovered from the f_1 units of gear, the f_2 units of gear or will not have been recovered. The probabilities of the three possibilities are equal to:

$$\frac{qf_1}{F+X}\left(1-e^{-(F+X)T}\right)$$

$$\frac{q\rho f_2}{F+X}\left(1-e^{-(F+X)T}\right)$$

$$1-\frac{q(f_1+\rho f_2)}{F+X}\left(1-e^{-(F+X)T}\right)$$

respectively, where $F = q(f_1 + f_2)$. Given that a tag has been reported, the probability that it was taken by fishermen in the first class is then binomial, i.e.:

$$\Pr(s_1|s) = \binom{s}{s_1}\left(\frac{f_1}{f_1 + \rho f_2}\right)^{s_1}\left(\frac{\rho f_2}{f_1 + \rho f_2}\right)^{s_2} \tag{9}$$

which is completely analogous to the corresponding results for catch sampling, cf., equation (3).

The parameter q measures "catchability" which in actuality may vary considerably during a long season or over several seasons. If the time scale is divided into J intervals and $q(t) = q_j$ for $t_{j-1} \leq t \leq t_j$, $j = 1,2,\ldots,J$, it can be easily shown (following Chapman, 1960) that for a given tag the expected probability of recovery by the research agency by time $t = T_J$ is:

Pr(recovery by fisheries agency) =

$$\sum_{j=1}^{J} \frac{q_j(f_1 + \rho f_2)}{X + q_j F} e^{-\left(XT_{j-1} + F\sum_{i=0}^{j-1} q_i\Delta_i\right)}\left(1 - e^{-[X + q_j F]\Delta_j}\right) \tag{10}$$

where $\Delta_j = t_j - t_{j-1}$. By simply deleting ρf_2 in equation (10) we obtain an expression for the probability that the recapture was made by the fishermen in the first class. Thus the conditional probability of s_1 given s is again given by equation (9) showing that so long as the same fraction of the effort is inspected during each of the J intervals, variations in catchability can be ignored. Of course, the same statement also applies to variations in the number of units of gear since the fluctuations in the levels of fishing intensity could be incorporated in the parameter q.

COMPUTATION OF SAMPLE SIZE

The null hypothesis, H_0:$\rho = 1$, would be doubted if the proportion of tags recovered from the inspected class is too high in relation to the proportion of the catch or the amount of gear in this class. Using the normal approximation of the binomial distribution, the well known most powerful one-sided test would be to reject H_0 if $s_1 \geq s_R$ where:

$$s_R = z_{1-\alpha}\sqrt{sp_0q_0} + 1/2 + sp_0 \tag{11}$$
$$p_0 = \frac{f_1}{f_1 + f_2} \text{ or } = \frac{C_1}{C_1 + C_2}$$
$$q_0 = 1 - p_0$$

if this expression happens to be an integer. If it is not, s_R is taken to be the nearest integer which is larger. The power of the test against a specific alternative would be the probability of rejecting H_0 when $\rho = \rho_a < 1$. Again, approximating the binomial distribution by the normal, the number of recoveries needed to test H_0 at pre-set values of α and β for different ρ's can be expressed as:

$$s = \frac{\left(z_{1-\beta}\sqrt{p_1q_1} + z_{1-\alpha}\sqrt{p_0q_0}\right)^2}{(p_1 - p_0)^2} \tag{12}$$
$$p_1 = \frac{f_1}{f_1 + \rho f_2} \text{ or } = \frac{C_1}{C_1 + \rho C_2}$$
$$q_1 = 1 - p_1.$$

Values of s as a function of the reported ratio and the fraction of the total catch inspected, $C_1/(C_1 + C_2)$, or of the total effort, $f_1/(f_1 + f_2)$, for which the reporting is known to be complete, are given in Table I. The tabled values have low accuracy for small values of s where the normal approximation to the binomial distribution is not too close. These errors are of little importance for larger s's.

EXAMPLES

The following four examples will illustrate the use of Table I.

EXAMPLE 1

A biologist wants to be 99% sure of detecting non-reporting of 20% or more of the tags recovered by a commercial fishery. From past experience he knows that at least 30% of the tags released will be recovered. Twenty-five percent of the fishermen agree to attend a special course of instructions and cooperate fully in this experiment. If α (the probability of mistakenly concluding that the reported ratio, ρ, is less than 1) be set at 0.10, how many tags should be liberated?

SOLUTION: In Table I, for $\rho = 0.80$, $f_1/(f_1 + f_2) = 0.25$, $\alpha = 0.10$ and $1 - \beta = 0.99$, s is found to be 1340. To solve for t, the number of tags that must be put out when the 30% recovery estimate refers to recaptured but not necessarily reported tags, note that r, the number of tags we would expect to be recaptured, can be written $r = ut$, where u is the rate of exploitation (see Ricker, 1958, p. 20). Then s, the number of tags turned in, should be:

$$s = u\left(\frac{f_1}{f_1 + f_2} + \frac{\rho f_2}{f_1 + f_2}\right)t$$

Substituting the values given above:

$$1340 = 0.30\left(\frac{1}{4} + (0.80)\frac{3}{4}\right)t$$

$$t = \frac{4(1340)}{(0.30)(3.40)} = 5255$$

However, the 30% recovery estimate could have been based on the percentage of tags reported in the past. In this case, $\rho u = 0.30$ or $u = 0.30/0.80$. We now expect the number of tags reported to be:

$$s = \frac{0.30}{0.80}\left(\frac{1}{4} + (0.80)\frac{3}{4}\right)t$$

Solving for t:

$$t = \frac{4(0.80)(1340)}{(0.30)(3.40)} = 4204$$

The point of this example is that the tagging program should be designed to return at least 1340 tags to the research agency.

The second example illustrates a situation where there may be a differential between the costs of catch sampling and effort sampling.

EXAMPLE 2

A biologist wants to estimate the percentage of marks detected and reported by sportsmen and would like to be 90% sure of discovering a reported ratio of 80% or lower. Two thousand marked trout have been released in a large lake shortly before the opening of the fishing season and an unknown portion of them would be expected to survive until opening day. Assume:

(i) the unmarked and marked members of the population are equally vulnerable to capture;

(ii) a reliable estimate of the total effort and the total catch for each week of the season is available;

(iii) the "catchability" of the trout is constant within a week but may vary from week to week;

(iv) no immigration or reproduction occurs during the season and thus the size of the population in the lake declines steadily as the catch mounts.

The biologist must decide whether to sample the catch or the effort to estimate the reported ratio. We will consider sampling to be largely a problem of providing coverage for the areas of access to the lake and that the cost would be roughly proportional to the percentage of the total effort interviewed on a given day regardless of the numbers of fishermen involved. In such a situation it may be relatively inexpensive to sample 10% or 20% of the fishermen using the lake on a given day, but the costs would be expected to increase rapidly as the percentage of fishermen included in the sampling was increased.

The total number of fish recovered from sampling a fixed percentage of the fishermen would, of course, tend to drop in the latter part of the season because of the drop in the numbers of fish in the lake and the concomitant decrease in the numbers of fishermen. For example, the total catch during a 5-week season may be 100,000 but the majority of these fish, say 63,000, may be taken during the first week of the season. Sampling one-half of the effort expended during the first week (which represents a smaller portion, say 20%, of the total season's effort; e.g., if a total of 25,000 units of effort were expended during the entire season, 10,000 or 40% of these fished during the first week) would then provide 31.5% of the total catch. On the other hand, inspection of a straight 20% of the effort expended each week would be expected to yield only 20% of the catch. As the marked ratio remains constant the catch can be inspected anytime during the season. Clearly the optimum time to inspect the catch is during the first part of the season when both the intensity and catch per unit of effort are highest; we will assume the entire catch sample will be taken during the first week.

However, effort sampling is not so flexible. Because catchability and population size vary, a constant percentage of each week's effort must be sampled. Effort sampling does not require assumption (i) since only the relationship between the effort and the marked population is involved. However, (i) is replaced by the assumption that the percentage recovery is directly proportional to the fishing intensity in any interval.

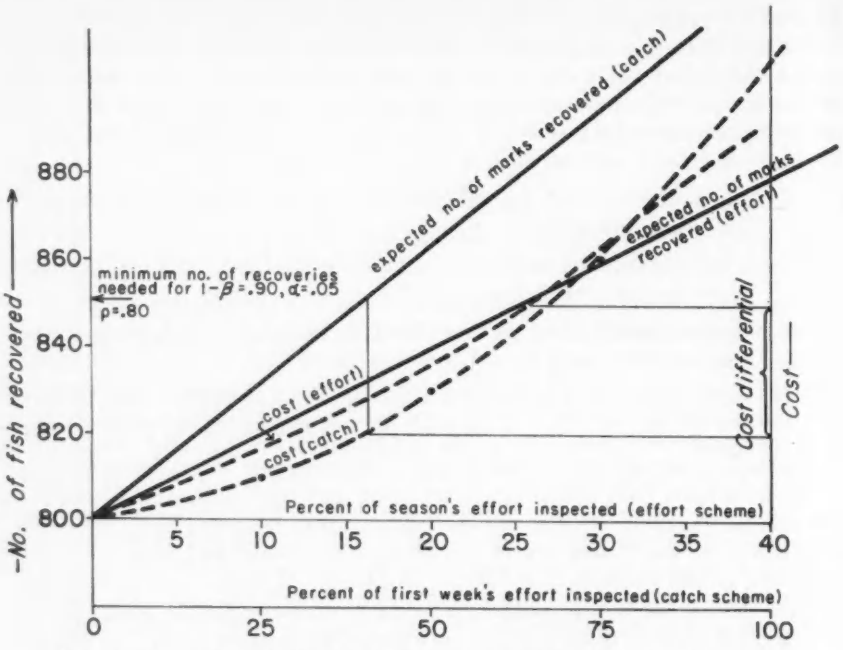

FIG. 1. Comparison of the costs of catch and effort sampling for a sports fishery.

The relevant factors that must be considered when evaluating the two sampling schemes are illustrated in Fig. 1. An arbitrary number (taken to be 1000 here) must be assigned to the expected total number of marked fish recovered to plot the two "expected number-of-recoveries" lines. The required number of recoveries was taken from Table 1, using $\alpha = 0.05$, $\beta = 0.10$, $\rho = 0.80$ for the optimum $f_1/(f_1 + f_2)$ and $C_1/(C_1 + C_2)$ ratios. For the cost curves shown, catch sampling is most economical. A different choice of cost curves might reverse the verdict.

The next two examples will illustrate the use of Table I in other areas of fisheries research.

EXAMPLE 3

Suppose the experiment described in Example 2 was carried out and reported ratio of unity was found. The following year the hatchery conducts an experiment to determine the advisability of early pre-season stocking as opposed to plants made just before the onset of fishing. Assume that if the trout can be released two months before the opening of the season, the capacity of the hatchery (and the number of fish stocked) can be increased by 10%. Thus if the survival rate of the early pre-season releases is greater than 0.909 an

increase in the catch should result from early planting (ignoring possible differences between the growth rates of early and late plants).

To estimate this survival rate ($= q$), N_E fish are released in the early plant and N_C fish in the late plant. Assume that the survival of the late plant is one[3] and that the hypothesis of interest is, $H: q = 1$, *vs*, the alternative $\bar{H}: q = q_1 < 1$. The probability of rejecting H should be high when $q_1 \leq 0.90$. Taking $\beta = 0.01$ and $\alpha = 0.05$, how many recoveries are needed and what is the approximate optimum ratio of $N_C/(N_C + N_E)$? The exact optimum ratio will usually lie between two of the ratios given in Table I. However, since in the neighborhood of the optimum ratio, the required sample sizes change slowly, the tabulated values will suffice for most practical purposes.

SOLUTION: In Table I for $\rho\ (= q) = 0.90$, $\alpha = 0.05$ and $\beta = 0.01$ the minimum number of recoveries is found to be 5684 when $N_C/(N_E + N_C) = 0.5$. If the expected recovery is at least 60%:

$$N_C + q_1 N_E = \frac{5684}{0.6}$$

Or, setting $N_E = N_C$:

$$N_C = \frac{5684}{(0.6)(1 + q_1)} = 4986$$

EXAMPLE 4

An experiment to determine if the survival rate of downstream migrant salmon is significantly reduced by passage over a dam might involve the release of one group (experimental) of fingerlings in the forebay and another group (control) in the tail-race of the dam. Fyke nets or other such gear would be employed some distance downstream to recover the fingerlings. Setting N_C and N_E equal to the respective numbers of controls and experimentals released, n equal to the total number of recoveries and q equal to the survival rate of the experimentals, test the $H: q = 1$ *vs*. $\bar{H}: q = q_1 < 1$. If the experimenter wishes to be 80% sure of detecting a mortality of 5% or greater and uses an $\alpha = 0.05$, how many recoveries are required?

SOLUTION: Entering Table I with $\rho(= q_1) = 0.95$, $\alpha = 0.05$, $\beta = 0.20$; n is found to be 9402 for $N_C/(N_E + N_C) = 0.5$. In this case the experimenter has the option of varying either the number of fingerlings released or the recovery effort to obtain the desired number of recoveries. The number of fish recovered may be proportional to the fraction of the total cross-sectional area of the stream covered by nets at the recovery site and, if so, the cost of recovering a given percentage of the fish released at the dam could then be easily computed. The relative costs of sampling and of obtaining and marking fingerlings would then determine the optimum allocation of funds to minimize the total cost of the experiment.

[3]A survival rate of 1 was assumed for simplicity. The method illustrated is equally applicable if the survival of the late plant was taken as γ where $0 < \gamma < 1$ and the null hypothesis and the alternative were $H: q = \gamma$ and $H: q = q_1 < \gamma$, respectively.

COMMENTS

The plan presented here for estimating incomplete reporting should not be confused with the plan of examining the catch for tags that the fishermen failed to remove. Such "posterior" examinations are quite valuable in helping to bridge the gap between the number of tags the fishermen catch and the number that are eventually returned to the research agency but do not measure nonresponse error.

Examination of the uninspected portion of the catch for tags not removed by the fishermen (supposedly the inspected portion of the catch will contain no tags) is a means of separating the incomplete reporting bias into its components. One component is the fisherman's failure to remove the tag from the catch and the other is the fisherman's failure to return recovered tags to the research agency.

The required sample sizes tabulated in Table I demonstrate the difficulty in detecting incomplete tag reporting even when a number of demanding assumptions are satisfied. The evaluation and interpretation of tagging results usually requires many more assumptions, e.g., that the immediate mortalities suffered as a direct result of the tagging operation are negligible, that the fish's normal behavior pattern has not been drastically altered by the application and presence of the tag, that the recovery gear is not selective for tagged fish, etc. In many cases the experimental results will not provide an adequate test of these assumptions. Careful advance planning and execution of tagging experiments are required if the results are to be meaningful. The design of the experiment must take into account the nature of the fish and of the fishery and the experiment should involve substantial numbers of fish and an extensive recovery operation.

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TABLE I. Number of recoveries needed for prescribed probabilities of detecting incomplete reporting with various levels of catch inspection. Symbols are defined on page 819.

$\alpha = 0.10$

p	$1-\beta$	$C_1/(C_1 + C_2)$ or $f_1/(f_1 + f_2)$									
		.05	.10	.15	.20	.25	.30	.40	.50	.70	.90
.25	.50	6	4	4	3	3	4	4	5	9	28
	.80	24	14	11	10	10	9	10	11	17	51
	.90	39	23	18	15	14	14	14	15	23	66
	.95	54	31	24	20	19	18	18	19	28	80
	.99	88	50	37	32	29	27	26	28	40	109
.50	.50	39	23	18	15	14	14	14	15	23	66
	.80	136	76	56	47	42	39	38	39	55	147
	.90	210	116	85	71	63	58	55	56	76	201
	.95	284	156	114	94	83	76	71	73	97	252
	.99	453	246	178	146	128	117	108	109	143	365
.60	.50	84	47	36	30	27	26	25	27	38	106
	.80	276	151	110	91	80	74	69	71	95	247
	.90	421	229	166	136	120	110	101	102	134	344
	.95	564	305	221	180	158	144	132	133	172	436
	.99	888	478	344	280	243	221	201	200	256	639
.70	.50	197	109	80	66	59	55	52	53	72	191
	.80	615	332	240	196	171	156	143	143	186	469
	.90	925	498	359	291	253	230	209	208	266	662
	.95	1230	660	474	384	333	302	273	271	342	847
	.99	1917	1026	734	593	513	464	416	410	513	1256
.75	.50	322	176	128	106	93	86	80	81	108	278
	.80	981	527	380	308	268	244	221	220	280	696
	.90	1468	787	564	456	395	358	323	319	402	990
	.95	1943	1040	744	601	519	470	422	415	519	1272
	.99	3016	1609	1148	925	797	720	643	630	781	1895
.80	.50	568	307	222	182	159	145	133	134	173	439
	.80	1688	904	647	523	453	410	369	364	457	1121
	.90	2512	1341	958	772	667	602	539	529	658	1603
	.95	3314	1767	1260	1015	875	789	704	689	853	2065
	.99	5120	2725	1939	1558	1340	1207	1073	1046	1285	3093
.85	.50	1130	607	436	354	307	279	252	250	317	787
	.80	3290	1754	1251	1007	868	783	699	684	847	2052
	.90	4866	2590	1844	1482	1275	1148	1021	997	1225	2950
	.95	6401	3403	2420	1943	1670	1502	1333	1298	1590	3814
	.99	9845	5227	3712	2975	2554	2294	2031	1972	2402	5733
.90	.50	2832	1512	1079	869	750	677	605	593	736	1789
	.80	8074	4289	3048	2444	2100	1887	1672	1626	1985	4748
	.90	11881	6305	4475	3585	3076	2761	2442	2369	2880	6859
	.95	15579	8261	5859	4691	4022	3608	3186	3086	3743	8894
	.99	23864	12643	8959	7166	6138	5501	4850	4691	5669	13423
.95	.50	12548	6658	4724	3785	3246	2914	2576	2499	3036	7227
	.80	35080	18573	13151	10513	8999	8060	7097	6855	8262	19515
	.90	51367	27181	19237	15369	13149	11770	10352	9989	12013	28320
	.95	67153	35522	25132	20072	17167	15362	13503	13020	15641	36822
	.99	102459	54175	38312	30586	26148	23389	20540	19791	23732	55778

TABLE I (continued)

$\alpha = 0.05$

p	$1-\beta$	$C_1/(C_1+C_2)$ or $f_1/(f_1+f_2)$									
		.05	.10	.15	.20	.25	.30	.40	.50	.70	.90
.25	.50	9	6	5	5	5	6	7	8	14	46
	.80	30	19	15	13	13	13	14	15	25	75
	.90	47	28	22	19	18	18	18	20	32	93
	.95	63	37	29	25	23	22	23	25	38	109
	.99	101	57	44	37	34	33	32	35	51	143
.50	.50	63	37	29	25	23	22	23	25	38	109
	.80	180	100	75	63	57	53	51	54	76	207
	.90	264	146	108	90	80	75	71	74	102	271
	.95	346	191	140	116	103	95	90	92	125	331
	.99	530	289	211	174	153	141	131	133	177	458
.60	.50	137	77	58	49	45	42	41	44	63	174
	.80	368	202	148	123	109	101	95	97	132	346
	.90	533	291	212	175	154	142	131	134	178	460
	.95	693	376	273	224	197	180	166	168	221	566
	.99	1048	566	409	334	291	266	243	244	315	794
.70	.50	324	178	131	109	97	90	85	87	119	315
	.80	827	448	325	266	233	213	196	197	257	653
	.90	1183	638	461	375	327	298	272	272	350	879
	.95	1524	820	590	479	417	379	344	343	437	1091
	.99	2281	1223	877	710	615	558	503	498	628	1549
.75	.50	530	289	211	174	153	141	131	133	177	458
	.80	1325	714	515	419	364	332	302	301	386	968
	.90	1883	1011	726	589	511	464	420	416	528	1310
	.95	2417	1296	929	751	651	590	532	525	662	1631
	.99	3600	1924	1375	1110	959	867	777	764	953	2328
.80	.50	935	506	366	299	261	239	219	220	285	722
	.80	2289	1227	880	712	617	560	505	499	630	1554
	.90	3234	1730	1237	999	864	781	701	690	863	2114
	.95	4137	2209	1578	1272	1098	992	888	872	1084	2641
	.99	6132	3268	2329	1874	1614	1455	1297	1269	1567	3788
.85	.50	1862	1000	718	582	506	459	415	412	523	1297
	.80	4473	2388	1705	1374	1185	1070	957	939	1166	2836
	.90	6287	3350	2387	1920	1654	1491	1329	1299	1604	3877
	.95	8016	4267	3037	2441	2100	1891	1682	1641	2018	4859
	.99	11827	6286	4468	3585	3080	2769	2456	2390	2922	7000
.90	.50	4666	2490	1777	1432	1235	1115	997	977	1213	2947
	.80	11012	5854	4162	3340	2871	2582	2291	2230	2730	6544
	.90	15398	8176	5807	4655	3997	3590	3179	3088	3764	8989
	.95	19572	10386	7371	5905	5066	4548	4022	3902	4743	11299
	.99	28752	15243	10808	8651	7415	6649	5870	5684	6886	16345
.95	.50	20671	10967	7782	6234	5348	4799	4243	4116	5000	11905
	.80	47983	25412	18000	14393	12324	11041	9727	9402	11345	26830
	.90	66770	35343	25021	19997	17114	15324	13487	13022	15682	27011
	.95	84619	44776	31689	25317	21660	19389	17053	16456	19791	46652
	.99	123797	65478	46319	36989	31632	28303	24871	23978	28788	67742

TABLE I (continued)

$\alpha = 0.01$

ρ	$1-\beta$	$C_1/(C_1 + C_2)$ or $f_1/(f_1 + f_2)$									
		.05	.10	.15	.20	.25	.30	.40	.50	.70	.90
.25	.50	17	12	10	10	10	11	13	16	28	92
	.80	45	28	23	21	20	20	22	25	42	131
	.90	65	39	31	28	27	26	28	32	51	155
	.95	84	50	39	35	33	32	33	37	59	175
	.99	126	73	57	49	46	44	45	49	75	218
.50	.50	126	73	57	49	46	44	45	49	75	218
	.80	278	157	118	100	90	85	83	88	127	350
	.90	382	213	158	133	119	112	108	113	159	432
	.95	479	266	197	164	147	137	130	136	188	506
	.99	692	381	280	232	205	190	179	184	250	661
.60	.50	274	154	116	98	89	84	82	87	125	347
	.80	578	319	235	195	174	162	153	158	217	579
	.90	781	428	314	259	230	212	199	204	276	723
	.95	971	531	387	319	281	259	242	246	329	855
	.99	1385	753	546	448	393	360	332	336	441	1131
.70	.50	648	357	262	218	193	179	169	174	238	629
	.80	1312	713	518	425	373	342	316	320	422	1083
	.90	1751	948	686	561	490	449	412	414	539	1368
	.95	2162	1167	843	687	599	547	500	500	645	1629
	.99	3048	1640	1180	959	834	758	688	685	874	2181
.75	.50	1060	578	422	347	305	281	261	266	353	914
	.80	2110	1140	823	671	586	535	489	490	633	1597
	.90	2802	1509	1087	883	769	700	636	634	811	2029
	.95	3446	1852	1331	1080	938	852	772	767	975	2424
	.99	4835	2591	1857	1503	1302	1180	1063	1050	1323	3261
.80	.50	1869	1011	732	597	522	477	437	439	570	1444
	.80	3661	1966	1413	1145	994	903	817	811	1029	2555
	.90	4834	2591	1857	1502	1301	1179	1063	1050	1323	3261
	.95	5927	3172	2270	1834	1586	1435	1290	1271	1593	3909
	.99	8775	4419	3156	2544	2196	1984	1775	1743	2169	5282
.85	.50	3724	2000	1437	1165	1011	918	830	824	1045	2593
	.80	7184	3840	2744	2214	1913	1729	1550	1524	1902	4647
	.90	9441	5038	3595	2896	2498	2255	2015	1976	2452	5957
	.95	11537	6150	4383	3528	3040	2741	2445	2393	2958	7161
	.99	16035	8534	6074	4882	4201	3782	3364	3283	4036	9719
.90	.50	9332	4980	3554	2863	2470	2229	1993	1954	2424	5894
	.80	17752	9444	6720	5398	4643	4178	3714	3621	4445	10689
	.90	23221	12342	8773	7040	6049	5438	4824	4695	5742	13759
	.95	28291	15027	10674	8560	7351	6604	5851	5687	6938	16586
	.99	39150	20774	14743	11812	10134	9096	8044	7804	9488	22601
.95	.50	41348	21937	15566	12469	10696	9600	8487	8232	10002	23813
	.80	77628	41128	29142	23312	19969	17897	15779	15263	18444	43682
	.90	101102	53539	37919	30318	25958	23254	20483	19795	23878	56448
	.95	122823	65021	46037	36797	31496	28206	24830	23981	28893	68223
	.99	169262	89565	63386	50642	43326	38784	34111	32916	39588	93317

The Light Pickle Salting of Cod[1]

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ABSTRACT

Salting theory for the light pickle salting of cod on a commercial scale is discussed and data are presented on the salt uptake with respect to time, temperature, and location in the tank. Variation of salt uptake by fish was examined and the proportion of top-quality fish, in terms of the amount of salt appropriate to the various commercial grades, that could be expected from a given salting operation is calculated. A method for determining an overall transfer coefficient is suggested and a coefficient for the case in point calculated. A regression line for water and salt contents of the fish during pickle salting is given.

INTRODUCTION

Salting preserves cod by restriction of bacterial and enzymic activity, and is usually followed by a period of drying. Many degrees of salting are practised, and before drying the fish may contain from 4 to 20% of salt by weight, depending on the particular cure desired. In general two major categories of salting exist, those of heavy and light salting. In the case of heavy salting, the salt content of the fish is not critical, as long as sufficient salt is present. Light salting is, however, a much more demanding procedure. Within this category several grades of fish exist. Each grade has associated with it a definite range of salt content. The higher the salt content, the less is its market value as a light-salted fish. Thus, in the preparation of top-quality fish, the producer is faced with the necessity of salting between relatively narrow limits, determined by the possibility of spoilage due to an insufficiency of salt, and by downgrading due to an excess. Although copious data are available on the principles of heavy salting of cod (Beatty and Fougère, 1957; McPhail, 1957), fewer data are available concerning the light salting of cod (Beatty and Fougère, 1957; van Klaveren and Legendre, 1958; Legendre, 1960). It is the object of this paper to study a typical light-salting operation in order that ideas and standards of comparison might be afforded for the evolution and evaluation of possible improvements on the current light-salting procedure.

The chemistry of fish salting is a complex topic, a detailed discussion of which lies outside the ambit of this paper. It is, however, desirable to review certain general technological ideas, and to develop some basis for comparison of data obtained under different conditions.

When a portion of cod muscle is placed in a salt environment, whether dry

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or in aqueous solution, it immediately tends to equilibrate with its surroundings. This equilibrium may be partly defined for practical purposes as an approximate equality of the brine in the fish (i.e. the amount of salt in the fish expressed as a fraction of the total salt and water in the fish) to that of the ambient brine (Reay, 1936; Jarvis, 1950, p. 39; Fougère, 1952). To complete this description of the system at equilibrium, it is necessary to establish the ratio of this internal brine to muscle, and hence the ratios of salt and water to muscle. These can vary in a complicated manner depending on the method of application of salt or concentration of ambient brine, due to a change, broadly referred to as denaturation, in a protein fraction of the muscle known as actomyosin (Duerr and Dyer, 1952). The latter constitutes some 75% of the total protein present in the muscle. Many factors can affect the denaturation process, notably salt concentration, pH, and temperature. Although the water-retention capacity of the fish protein can vary markedly in dilute brines and for low internal salt concentrations, a critical internal salt content exists in the region of 8% (percentage salt on wet basis), above which the protein is denatured rapidly and salt gain is accompanied by water loss. In commercial practice, dry salt is usually employed. The lightest degree of fish salting involves the addition of an amount of dry salt sufficient to ensure denaturation if the system is allowed to come to equilibrium.

Throughout the course of a dry-salting operation, the average water concentration in a fish inversely follows its average salt concentration. The rate of salt uptake is in constant ratio to the rate of water loss. This would seem to hold even if only a small quantity of salt is taken up by the fish. The implication is that salt and water exchange is largely confined to the region of denatured muscle. Thus we have a picture of a "front" at which denaturation occurs, moving into the muscle. Ahead of this "front", the salt penetration is relatively insignificant; behind it, the bulk of the salt and water exchange takes place. Such evidence is afforded by curves showing the average salt content of a thick fish, and the salt content of its central region, as functions of time (Dyer, 1942; Duerr and Dyer, 1952). During the first day a very marked difference in slope is apparent between the two curves. The average salt content of a light-salted fish may be as low as 4%. It is important to note that most of this salt is in a denatured region extending inward from the surface. It is obvious that the question of denaturation rate is of considerable importance in deciding the overall speed at which salting occurs. Available data indicate that denaturation occurs rapidly as soon as sufficient salt is present, and that temperature has no noticeable effect on this rate in the ordinary range of salting temperatures, say 32 to 60°F (0 to 16°C) (Duerr and Dyer, 1952).

Some retardation in the rate of penetration of salt occurs in the lower part of this temperature range. Few data are available on the effect of pH in the present context. In the work described in this paper control of pH was not attempted. Throughout the greater part of the salting time the pH value lay in the range 6.5 to 7.0. Conditions were similar to those under which the above denaturation work was carried out and also to those described by Castell (1953) in work on storing of light-salt cod in its own brine.

In the present discussion, the term "salt" is assumed synonymous with sodium chloride. The experimental work described below was based on the commercial Turks Island salt commonly employed in the industry. On the average this salt usually contains some 4% of impurities, primarily salts of calcium and magnesium (Hess, 1942). These tend to retard the penetration of sodium chloride (Tressler, 1919). It is unlikely that significant differences will result in comparison with other solar salts which tend to be similar with respect to contamination. Some significant discrepancy would probably be encountered in comparison with results of employing pure sodium chloride.

The data of Reay (1936) and Dyer (1942) indicate an exponential approach to equilibrium of the fish brine concentration with the ambient brine that forms during salting. For a great part of the overall salting period the fractional approach to equilibrium appears to be the same whether a light- or heavy-salting operation is being carried out. It seems reasonable, for practical purposes, that throughout a considerable part of the salting time the driving force during salting might be taken as the difference in concentration between the average internal fish brine and the ambient brine. If the extent of the latter is sufficient to remain virtually unchanged in concentration throughout salting, the resulting situation is analogous to "Newton's Law of Cooling". In the case of light salting, where a limited quantity of dry salt is employed, the picture is more complicated, since the concentration of the ambient brine formed changes not only through salt and water exchanges with the fish, but also as more of the undissolved salt goes into solution.

By the following method the overall transfer coefficient characterizing the resistance to salting under a given set of circumstances may be calculated. This affords a convenient means of comparison for the effects resulting from changes in the operating variables. The fundamental rate equation may be stated as follows:

$$\frac{dC_f}{dt} = K(C_b - C_f)$$

where C_b and C_f are respectively the ambient and fish brine concentrations, and K is the overall transfer coefficient. Integration of this equation, and its solution over a particular time interval, as indicated by the subscripts 1 and 2 to t, yields the following expression:

$$K = \frac{\log_e \frac{C_{f_2}}{C_{f_1}}}{\int_{t_1}^{t_2} \frac{C_b}{C_f}\, dt - (t_2 - t_1)}$$

It is convenient to solve the integral in the denominator graphically. This may readily be done since experimental values of C_b and C_f at particular times may be determined and it is only necessary to plot the ratio as a function of time and apply Simpson's rule. (K actually varies with time. Integration produces

an overall mean value. Theoretically it is possible to examine the variations of K with time by measuring slopes at different points. This is unsatisfactory unless a large number of points are available to define the curve and the slopes accurately.) Values of this coefficient for the particular case in hand were worked out and are presented later.

EXPERIMENTAL METHODS

The investigation was carried out by observing the changes in salt uptake by post-rigor fish at different levels in salting tanks left undisturbed at constant temperature for various periods of time. All the fish used were caught by an off-shore longliner and were gutted at sea. Salting was carried out within 24 hours of death. In the experiments, split fish weighing 1½ to 2½ lb (0.7 to 1.1 kg) were placed in aluminum tanks 4 feet wide, 4 feet long and 3 feet deep (1.2 × 1.2 × 0.9 m), each layer being salted by weight, using 10 lb (4.5 kg) Turks Island salt to every 100 lb (45 kg) of fish. The actual salting operation occupied some 2 hours, the brine forming rapidly and reaching the top layers of fish within a further period of about 2 hours. The total weight of fish in each tank was usually of the order of 2700 lb (1200 kg). During the salting operation, sets of ten tagged samples were distributed in regular pattern at each of seven different layers in the tank. Tubes were placed on top of each of these layers so that brine samples could be withdrawn for testing. These also afforded an approximate means of checking temperatures throughout the tank. A wooden rack loaded with weights was used to keep the upper layer of fish immersed after formation of the brine. The experiments took place in constant-temperature rooms at 42°F (5.6°C) and 58°F (14.4°C). When necessary the fish were spread for a short time to come to room temperature before being placed in the tanks.

Moisture contents were determined by drying representative samples of the muscle from a given fish for 24 hours at 221°F (105°C). Salt contents were estimated by determining the electrical conductivity of an aqueous extract of the dried residue remaining after the moisture determination. The salt value obtained from a predetermined calibration curve was then corrected for a blank value for unsalted fish muscle. The blank value was based on estimates on fifty fish of varying post-mortem times and history, and as determined in this manner had a value equivalent to a salt content of 0.8%. The standard deviation proved less than 0.07% and was deemed insufficient to invalidate the method in its present context.

RESULTS

Variation of Salt Penetration with Depth

After various periods of immersion in the tank at 42°F, marked differences in salt uptake were noted between the top, bottom, and central regions. This is illustrated in Fig. 1 where layer 1 represents the top, and layer 7 the bottom layer of fish in the tank. Each point represents the average value of salt content for ten fish from a given layer. The significance of these results is shown by the

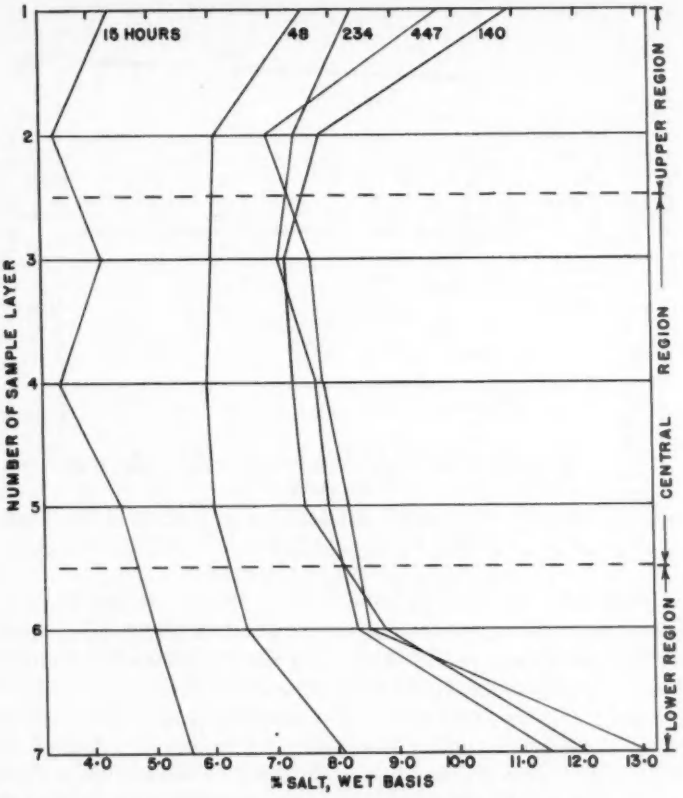

FIG. 1. Mean salt penetration into fish at different levels in a salting tank after various periods of salting.

fact that a standard error of the mean calculated from the greatest standard deviation encountered in any of these sets of ten samples from a given layer was 0.4%, a figure considerably less than the general differences existing between the different regions of the tank. The mean salt content of the fish from different layers tended to show high values in both upper and lower regions.

Though a higher salt concentration at the bottom of the tank might well be expected, the fact that a similar condition occurred at the top is not so readily explicable. Above the surface layers of fish, which were kept immersed by a rack and weights, there existed a few inches of free brine. It was probably the building up and existence of this reserve of adjacent brine which permitted the upper layers to attain initially higher salt contents.

A similar pattern was observed at 58°F although a shorter series of immersion periods was occasioned by more rapid spoilage of the fish.

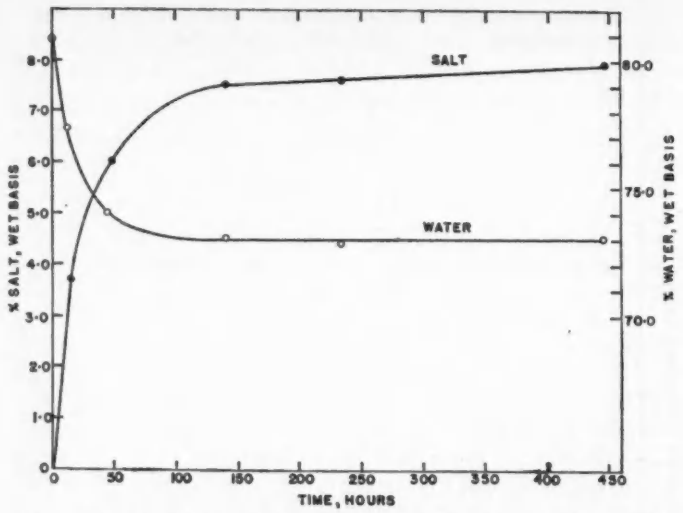

FIG. 2. Variation of salt uptake and water loss for the bulk of fish in the central region of the tank at 42°F.

MEAN RATE OF SALT UPTAKE FOR THE CENTRAL REGION OF THE TANK

The similarity of values observed for layers 3, 4 and 5 led to their being plotted as a single average in Fig. 2, showing the overall uptake of salt and loss of water for the central bulk of the fish. The standard deviation for a series of samples placed in a given layer was close to that obtained when a single average value for the three central layers of samples was employed. After 6 days, the bulk of the salt and water transfer had taken place. For split fish of similar size, placed in an excess of dry salt, Dyer (1942) has shown that about the same time is required to reach a like degree of approach to equilibrium.

CHANGES IN BRINE CONCENTRATION

In most experiments, records of brine concentrations were maintained. In Fig. 3, curve A shows the variation with time of the mean value of brine concentration for the upper six levels in the tank. These values differed little from layer to layer. Curve B refers to the brine concentration immediately above the bottom layer of fish. These curves are typical of the general behaviour of the brine in the tanks. For the first 2 days, the bottom layer shows something of an increase, commencing then to diminish at a rate similar to that in the rest of the tank. When comparing the rates of change in Fig. 2 and 3 it is well to bear in mind that the ratio of brine to fish in the tank was of the order of 1:3 and that small concentration changes in the fish reflect larger changes in the brine. It is apparent that the curve for the brine concentration in the bulk of the tank is approaching the region of 12 to 13%. This agrees with the final overall brine concentration in the system predicted by consideration of the total salt and water

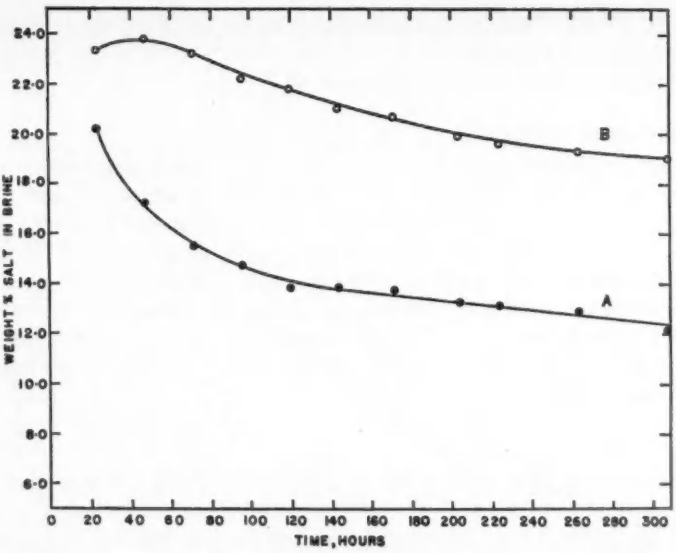

FIG. 3. Curves showing the mean value of brine concentration for A, the six upper levels, and B, the lowest level.

in the system and equality of internal fish and ambient brines at equilibrium. Direct measurement was also made of this quantity by weighing the total brine formed in an experiment, mixing it and observing its concentration. The result was in agreement with that expected.

After a period of about 300 hours, the brine concentrations throughout the tank became prone to a disturbance affecting all levels. The cumbersome nature of the experiments and limited practical significance did not warrant a close examination of this phenomenon. It was probably associated with the major pH change which occurs when fish are held under pickle for lengthy periods of time (Castell, 1953).

SALT TRANSFER COEFFICIENT

Using the equation described above, salt transfer coefficients were calculated for the common range of commercial light-salting time, which is usually about 48 hours. These values are given in Table I. The coefficients are based on the

TABLE I. Overall transfer coefficients for a single fish, as calculated for the experiments at 42°F.

Period	Coefficient
hours	
10 to 20	6.4×10^{-3}
20 to 30	6.9×10^{-3}
30 to 40	6.1×10^{-3}
40 to 50	$6.2\frac{1}{2} \times 10^{-3}$

data of Fig. 2 and 3, and are applicable to a single fish from the central region of the tanks. Unfortunately sufficient data were not available to determine similar coefficients for the use of salting at 58°F.

Effect of Temperature

A number of experiments were carried out at 58°F but this higher temperature was found to have relatively little effect on the rate of uptake of salt. It was noted that in general the uptake of salt by fish in the upper and lower regions was about 1 to 2% higher, and in the central region about 1 to 2% lower, than for the corresponding time at 42°F. Corresponding changes occurred in the brine, the concentrations at the bottom being a little higher, and in the central region of the tank a little lower, than in the experiments at the lower temperature. Due to the problem of spoilage, it was not desirable to continue experiments for longer salting periods.

Effect of Fine Salt

In one experiment at 42°F, finely ground Turks Island salt was used rather than the coarse salt employed in the other experiments. This yielded no clearly discernible improvement on the variability of salt uptake observed in experiments with coarse salt. A marked effect was observed, however, in that the disparity between the salt uptake of the central region and that of the lower regions was greatly reduced. High values were still obtained in the upper region of the tank. The salt uptake for the central region was consistent with that which would have been predicted for coarse salt as taken from Fig. 2. Thus, grain size of salt in dry salting would seem to have little effect on the rate of salt uptake. This is consistent with Bitting's (1911) observations.

Effect of Depth

In general the experiments were carried out using depths of fish slightly under 3 feet (1 m). One experiment was carried out in which the depth of fish was 18 inches (0.5 m). The same discrepancy was observed as in the case of the greater depths of fish: excessive salt penetration took place in the upper and lower regions as compared with the central region.

Salt and Water Regression Equations

It is apparent from Fig. 2 that the water and salt transfer are in a close inverse ratio. On a basis of analyses for salt and water on representative samples from each of 860 fish immediately following removal from the salting tanks, the following regression equations were calculated, yielding a correlation coefficient of 0.93:

$$S = 61.12 - 0.74M \text{ (standard error of estimate } = 0.7)$$
$$M = 81.83 - 1.19S \text{ (standard error of estimate } = 0.9),$$

where S and M are respectively the percentage of salt and moisture expressed on a basis of wet weight. Similar correlations with different constants result if a

dry, salt-free basis is employed. The line showing the estimated amount of salt associated with a given water content, with confidence limits at 80 and 95%, is given in Fig. 4. Points A to E, corresponding with the average water and salt

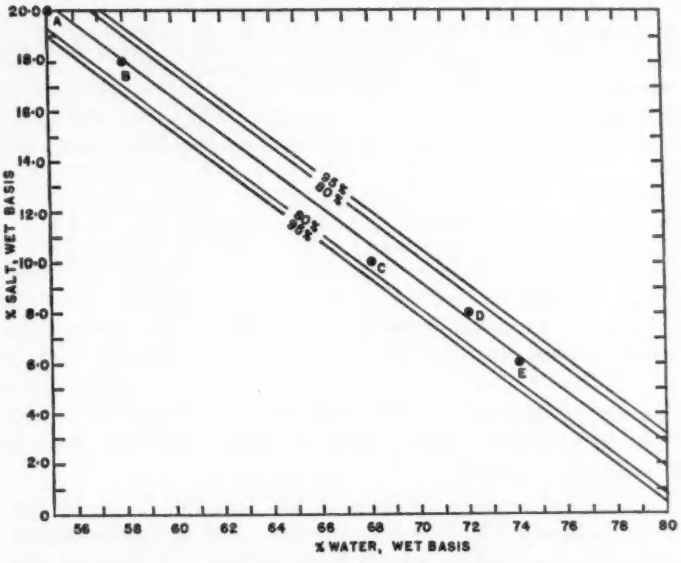

FIG. 4. Regression line of salt on water with confidence limits at 80 and 95% with points corresponding to the average accepted salt and water contents of Canadian salt cod products as follows: A, kenched heavy-salt fish; B, pickled heavy-salt fish; C, Newfoundland kenched light-salt fish; D, fall Gaspé cure; E, Gaspé cure.

contents of the various categories of salted fish produced in Eastern Canada, as reported by van Klaveren and Legendre (1958), demonstrate conformity of the line with general experience. The water content of fresh cod, as predicted by the intersection of the line with the appropriate axis, is 83%. This is somewhat higher than the usually accepted water-content value of about 81%, although the latter is subject to a good deal of uncertainty. In the case of four samples of fresh cod, for instance, Shewan (1944) has reported values ranging from 81 to 84%.

It is of interest to note that the only difference in respect to final water content between kenched cod and pickle-salted cod is that the former tends to have a slightly lower content. This is readily explicable in terms of evaporative losses.

An important aspect of this regression relation lies in the fact that, provided the fish are allowed to come to equilibrium with the salt environment, the average salt content of the fish may be predicted with reasonable accuracy for any of the amounts of salt usually employed in commercial operations.

Variation in Salt Content among Samples from Central Region of Tank

The amount of variation of samples withdrawn from the central region of the tank is a useful index of the degree of uniformity of product that may be obtained in this method of salting. Table II shows the mean values of salt content for the three central layers of samples which were used to plot Fig. 2, together with corresponding standard deviations and confidence limits at 80 and 95%.

Table II. Mean values of salt content for three central layers with their standard deviations and confidence limits for experiments at 42°F.

Brining time in hours:	15	48	140	234	441
		percent salt in fish from central layers			
Mean value	3.7	6.0	7.5	7.5	7.9
Standard deviation	0.7	0.6	1.1	0.8	1.2
80% of the fish lie between	2.5 – 4.9	5.1 – 6.9	5.8 – 9.2	6.3 – 8.7	6.0 – 9.8
95% of the fish lie between	2.3 – 5.1	4.8 – 7.2	5.4 – 9.6	5.9 – 9.1	5.5 – 10.3

No trend with time or increased temperature toward greater uniformity of salting could be observed. Similar standard deviations were noted for upper and lower regions of the tank.

It is of interest to compare these values with the ranges of salt content normally associated with the commercial grades of fish in Newfoundland. These latter are usually expressed on a basis of dry weight. If, however, the amount of moisture associated with the given salt content of a fish be obtained from the correlation referred to above, we may express these weights in terms of the salt contents on a wet basis at the completion of salting, on the assumption that the water loss is due solely to the action of the salt. These data are listed in Table III.

Table III. Relation between salt content on dry and wet basis at the end of salting.

Grade	Salt content	
	Dry basis	Wet basis
	%	%
Choice	18 – 21	4.0 – 5.0
Prime	21 – 24	5.0 – 6.0
Madeira	24 – 28	6.0 – 7.6
Thirds	28 – 31	7.6 – 9.1

From Fig. 2 it is seen that after a period of 24 hours, the mean salt concentration of the fish in the central region of the tank should have attained 4.6%. If the standard deviation is assumed to be 0.7%, as seems reasonable from Table II, then we may expect that 48% of the fish in the central region will achieve

Choice grade. If, on the other hand, we leave the fish in the tank for 35 hours, 83% of the fish in the central region will be within the top two grades, Choice and Prime. These percentages are based on the mean and limiting values of salt concentration, for the grades Choice and Prime as shown in Table III. Assuming a normal distribution and the appropriate standard deviations as obtained from Table II, the proportions of fish within the specified limits are easily calculated with the aid of a probability table. On the basis of the data available, estimation of the grades of fish in the top or bottom regions of the tank is somewhat speculative, but after a period of some 35 hours the fish in these regions, comprising about 50% of the total fish, should be primarily in the grades Madeira or Thirds.

DISCUSSION

The main problem confronting the salt fish producer is to salt fish within relatively narrow tolerances. The difficulties involved in doing this on a commercial scale are abundantly illustrated by the above data, based on experiments in which salting was carried out by careful proportioning of salt to fish of selected weight, the fish all being in good condition. The best result that could be anticipated, assuming that 50% of the total fish is in the central region, is about 40% in the top two grades. It is useful to compare this with Newfoundland light-salt fish production in general. Table IV shows the proportions of light-salt cod in

TABLE IV. Percentages of light salted exports by grade.

	Newfoundland exports		Bonavista exports	
Grade	1954	1955	1954	1955
	%	%	%	%
Choice	1.5	3.7	7.4	9.6
Prime	2.8	6.8	28.2	30.2
Madeira	49.2	51.4	34.8	33.5
Thirds	35.2	26.0	24.2	21.4

the two top grades produced during the years 1954 and 1955. For purposes of comparison values are also given for the Bonavista Experimental Plant (Conboy, 1957). It is interesting to note the agreement of the above-mentioned value of 40% with the corresponding 1955 value of 39.8% for Bonavista. The excellence of this agreement is to some extent fortuitous since no account has been taken of differences in production procedures. At Bonavista, the variation of fish size and downgrading due to faulty splitting may have been offset by the fact that the tanks used there were 2 feet deeper than those employed in the present work.

The biggest factor affecting the uniformity of salt uptake is that of fish surface area available for salt transfer. Schmidt (1952) has observed in the case of brined herring that variation in salt uptake cannot be explained in terms of fish thickness and fat content. Thus for improvement in the yield of top-quality fish, a very desirable factor is increase in the area of the fish surface

accessible to the brine. Circulation of saturated brine instead of dry salting would afford an excellent means of control of salt uptake and also, by passing the brines through a heat exchanger, of temperature. This is an important factor in summer conditions. The question is one, however, to be answered on economic grounds. Less elaborate and more in line with current practice, the use of deeper tanks, finer salt, or an arbitrary distribution of salt, are worth investigating. It is of particular interest that uniformity of salting cannot be increased by prolonging the salting time.

Of some assistance is the idea of a constant fractional approach to equilibrium independent of the amount of added salt. The salt content of the fish at equilibrium may easily be estimated from the assumption of equality of brine concentrations, the water and salt regression relation, and the overall water and salt content of the system. Thus, for example, if the salt content of heavy-salt fish at equilibrium is assumed to be 20%, and that of the light-salt fish prepared under the conditions described in this paper is 12%, after 24 hours some 50% of the total transfer will have occurred, the salt content in the first case being about 10% and in the second 6%. This may be seen by comparing Fig. 2 with the curve published by Dyer (1942) for heavy salting of fish of about the same size. More data are, however, desirable.

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The Partial Desalting of Salted Cod[1]

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ABSTRACT

The results of small-scale experiments on the desalting of heavy-salted cod are presented. A method is proposed for a commercial desalting operation.

INTRODUCTION

Interest has been shown in utilizing the better keeping qualities of heavy-salt bulk cod as compared to light-salt cod, and a desalting process prior to drying, as aids to light-salt fish production where circumstances render prompt drying of the fish difficult. This is a problem of some complexity. Any general practical solution requires a large number of possible initial salt and water contents of the heavy-salt bulk to be considered in setting up the desalting procedure. It is also important that the fish at the end of desalting shall be reasonably uniform in salt content. Complete desalting of the surface is conducive to ready spoilage.

Two possible desalting methods are feasible. The first method involves brief periods of immersion of the heavy-salt bulk in fresh water, followed by periods of press-piling to permit diffusion of salt in the muscle to the salt-depleted region. This is laborious and involves substantial risk of spoilage. The second method constitutes a considerable improvement and entails immersing the heavy-salt bulk in a limited quantity of fresh water, and allowing the whole to come to equilibrium. This method will be elaborated below.

EXPERIMENTAL

In the present work, a series of experiments was carried out to determine the general characteristics of a desalting procedure. Rectangular blocks of muscle were cut from heavily salted cod obtained from a commercial producer. The water and salt contents were determined on samples removed from parts of the fish adjacent to the block. The water was determined by drying to constant weight at 105°C. Salt was measured by potentiometric titration using a glass–silver/silver chloride electrode pair. The block was suspended by means of a wire stirrup in a vertical tared cylinder containing a quantity of water. At intervals throughout the experiment the block and the cylinder were each weighed and a small aliquot of ambient solution was removed for salt analysis. This enabled the water and salt exchanges to be readily followed. Agitation was carried out in different rooms, each at a controlled temperature. The results of this work are summarized in Table I.

On the basis of the results obtained from these experiments the work was repeated on a larger scale using 50-lb batches of fish. These were placed in a shallow tank, the desalting water being slowly circulated by means of a pump

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from one end to the other. Closed-circuit pumping of this nature allied to summer conditions engendered a temperature increase sufficient to reduce the first batch of fish to an unpleasant paste. Thus a modest degree of cooling was incorporated in further experiments by means of a small refrigeration unit and cooling coils immersed at either end of the tank to prevent the temperature rising beyond the critical region of about 80°F. To ensure adequate circulation of water between the fish, longitudinal wooden slats, of 1- by ½-inch cross-section were used to space the consecutive layers.

The rate of desalting is primarily dependent on the volume of desalting water, temperature, agitation, and fish size. The results of a series of experiments in connection with these factors, using standard sized blocks of fish muscle, are shown in Table I. These results have been expressed in terms of the numbers of hours to reduce the salt content of the fish to 8, 6, and 4% respectively. Although the experiments were carried out on a small scale, they were found to constitute a useful basis for estimating the performance of large-scale systems involving batches of split fish. Although shorter desalting times result from the use of a large water volume, the advantage is not so great but that it is readily offset by the more uniform final salt distribution associated with an equilibrium process. The effect of temperature is marked, a drop from 75 to 37°F approximately doubling the time required for the same degree of desalting. Agitation can decrease desalting time but hardly to a degree that would warrant elaborate equipment.

RESULTS

When fish are placed in dry salt and allowed to come to equilibrium in their own pickle, it is found that the concentration of brine in the fish (i.e. the salt in the fish expressed as a fraction of their total salt and water content) effectively equals the concentration of the brine surrounding them (Fougère, 1952; Reay, 1936). It has also been found that the salt taken up by the fish at any time during the salting is in simple proportion to the amount of water lost (Crean, 1961). Thus if the percentage of salt in a fish at any time during salting is plotted against the corresponding percentage of water, the points will be on a straight line. It was found in the present work on desalting that a similar type of behaviour is encountered, the water and salt exchange being in simple proportion and proceeding to an eventual equality of brine concentration throughout the system.

DESALTING METHOD

We now have the means to postulate a simple method for a commercial desalting procedure. Consider Fig. 1. The right-hand scale states the quantity of dry salt to be added to 100 lb of fresh fish which, when allowed to equilibrate in its own pickle, will give a salt content on a wet basis exactly opposite on the left-hand scale. Consider then a batch of fish with water and salt contents depicted by the co-ordinates of point A. Prolonged storage will result in moisture loss and increase of the percentage wet weight of salt in the fish. During storage, the water and salt contents will progress along AB. Suppose the batch is weighed and found to have lost 25% of the weight it originally had at A. This

TABLE I. Summary of the effects of different variables on partial desalting

Primary variable	Temp.	Initial block dimensions	Salt and water content (on wet basis)				Volume of desalting water	Degree of agitation	Desalting time to attain salt content of			Slope of desalting line
			Initial state		After 24 hr							
			Salt	Water	Salt	Water						
	°F	cm	%	%	%	%	ml		8% hours	6% hours	4% hours	
Volume of	75	2 × 2 × 10	16.9	49.8	1.1	72.7	3000	Mild	3.0	5.5	9.0	0.69
desalting	75	2 × 2 × 10	16.9	52.2	3.0	73.5	195	Mild	3.1	6.0	12.2	0.62
water	75	2 × 2 × 10	17.0	51.6	4.7	73.3	100	Mild	3.6	8.1	. . .	0.65
Temp. effect	37	2 × 2 × 10	16.2	49.8	4.9	69.8	136	Mild	6.7	13.3	. . .	0.61
(small volume	75	2 × 2 × 10	16.2	49.8	3.6	70.3	136	Mild	3.1	6.2	15.5	0.61
of desalting	37	2 × 2 × 10	17.0	51.6	5.6	73.1	100	Mild	6.4	15.7	. . .	0.63
water)	75	2 × 2 × 10	17.0	51.6	4.7	73.3	100	Mild	3.7	8.2	. . .	0.65
Block size	75	2 × 2 × 10	16.9	52.2	3.0	73.5	195	Mild	3.1	6.0	12.2	0.63
(small volume)	75	3 × 3 × 10	16.9	52.2	4.0	71.8	365	Mild	5.8	11.0	23.5	0.63
Agitation	75	2 × 2 × 10	16.2	49.8	4.0	70.0	136	Mild	3.1	6.2	20.0	0.63
(small volume)	75	2 × 2 × 10	16.2	49.8	3.6	70.3	136	Strong	3.7	7.5	14.2	0.61

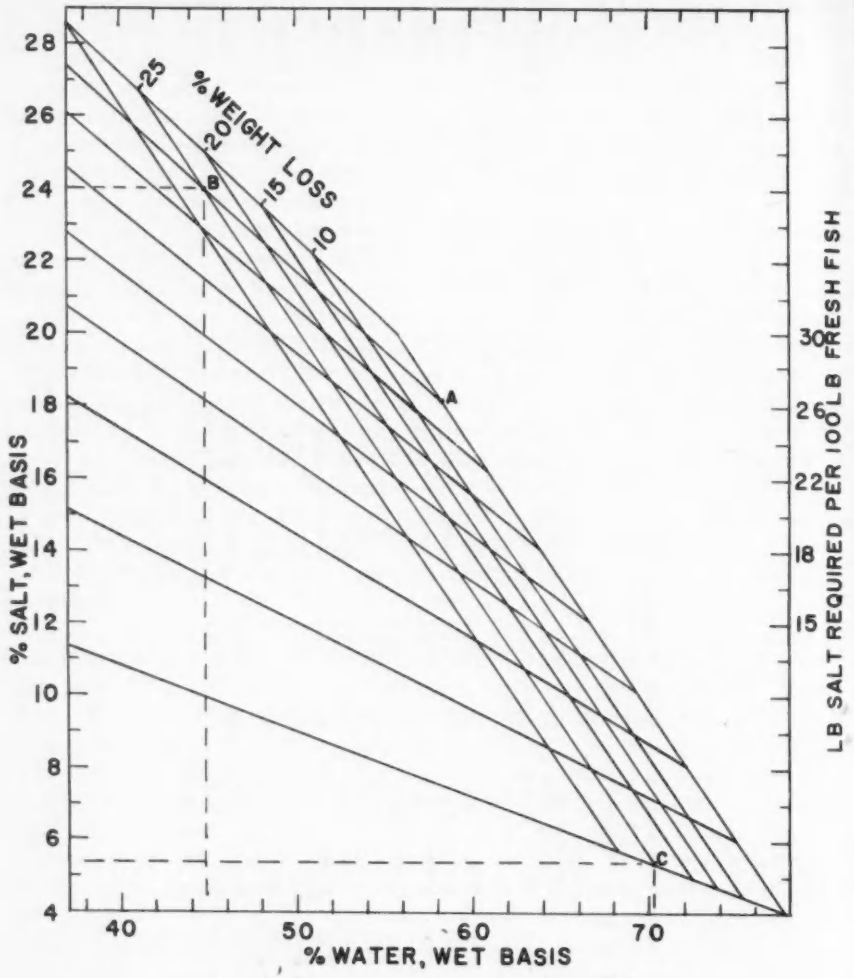

FIG. 1. State diagram for salting and desalting of fish muscle.

locates point B. Consider for example, 100 lb of fish containing 24% of salt and 44.8% water. This corresponds to point B. Suppose it is desired to reduce the salt content of this fish to 5.4% with a water content of 70.3% This corresponds to point C. The required amount of water may be estimated by means of the nomograph in Fig. 2, where scales X and Y are respectively the initial percentage salt and water contents of the fish, and scales X′ and Y′ are respectively the final salt and water contents when the system has come to equilibrium. The nomograph is used in the following manner. Draw a straight line through the

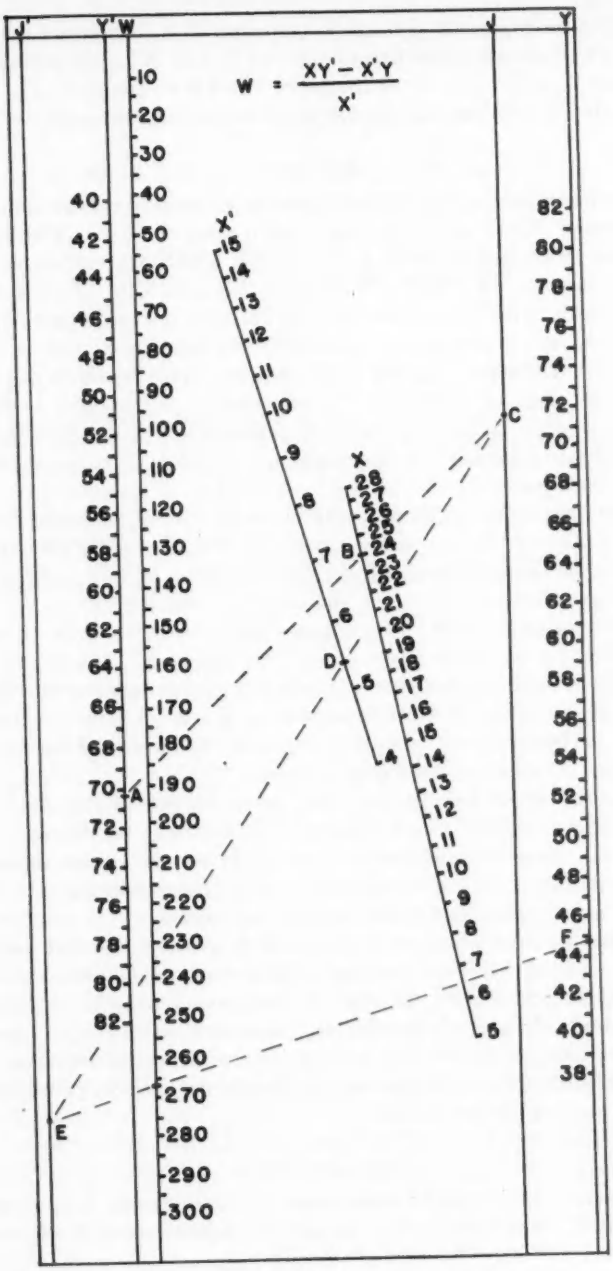

FIG. 2. Desalting nomogram.

points A (70.3 on Y′) and B (24.0 on X), and extend it to intersect the line J at C. From point C draw a straight line to point D (5.4 on X′), and extend it to intersect the line J′ at E. Join E to the point F (44.8 on the scale Y). The intersection of the line EF with the scale W gives the amount of water, 267 lb, to be added.

DISCUSSION

To test the efficacy of the method, some experiments were carried out on 50-lb batches of heavy-salted cod. The results proved satisfactory. Thus for example, salt analyses of six fish removed from a batch which was calculated to have a final salt content of 5.0% were: 5.0, 5.1, 5.0, 5.0, 5.0, 5.2% Elaboration of this larger-scale work to include factors affecting rate was not undertaken at this time.

In setting up a commercial-scale desalting operation, one of the major difficulties is that of separating the layers of fish. Many methods might be tried, as dictated by the costs involved. In experiments carried out at this Station longitudinal wooden battens of ½-inch thickness when placed between adjacent layers were found effective. This permits a ready flow of water down the tank between the layers of fish.

It sometimes happens that the desalting water added is insufficient to cover the fish. In this case the calculated amount of desalting water should be added, followed by a quantity of brine of strength the same as that anticipated when the system has come to equilibrium, sufficient to cover the fish.

With respect to agitation, the principal factor is to avoid the accumulation of a strong brine in the lower region of the desalting tank. If a simple recirculatory pumping system is employed, it is important to remember that continuous operation may lead to a rise in temperature sufficient to ruin the fish. Piping connections on the suction side of the pump must be tight, and the suction inlet well submerged, or excessive foaming will result.

In carrying out a desalting operation, measurements of the specific gravity of the desalting water afford a simple means of determining the degree of approach to equilibrium. Dissolved protein was not found to affect these measurements to a significant degree. Once the specific gravity of the desalting water becomes reasonably constant, the fish may be removed for drying.

The procedure outlined above is believed to afford a rational basis for the setting up of a salting–desalting process. The salt concentrations to be employed will be largely determined by the storage conditions available and the type of product required. It is recommended that operators setting up a process pay particular attention to the specific gravities of the desalting water as an index of the degree of completion. Thus a regular routine may be set up on an empirical basis for any given set of conditions.

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Chemical Characteristics of Salted Cod[1]

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ABSTRACT

A study has been made of the formation of decomposition products in three different types of salted codfish. The total volatile acids, trimethylamine, ammonia and free α-amino acids were determined on 50 samples of each type of salted fish. The total volatile acids and trimethylamine were found to be chemical indices which enable a clear differentiation between light- and heavy-salted cures. The presence of large quantities of these two decomposition products is typical of light-salted cures, especially of the "Gaspé cure".

The influence of the degree of salt saturation in the brine and in the muscle itself during processing, on formation of decomposition products, is discussed.

INTRODUCTION

The technology of salt curing of codfish has not been studied exhaustively and consequently salted cod has remained a product of frequently uneven quality, sometimes unattractive to the customer, although it is an inexpensive source of protein-rich food. Some of the aspects of processing salted cod were reviewed by Beatty and Fougère (1957) and by van Klaveren and Legendre (1958), and a selected bibliography of salted cod was recorded by McPhail (1957).

This paper forms part of a study on the chemical transformations in the flesh of salted cod during processing. The attempted purpose is to characterize, and to define chemically, a few types of Canadian Atlantic Coast salted cod.

The formation of a number of substances in unsalted cod muscle has been investigated to evaluate the state of spoilage of fish. Recently, it has been shown by Hillig *et al.* (1958), in a comparative study of the chemical indices of decomposition of cod, that (total) volatile acids number, formic and acetic acids, (total) volatile bases, (total) volatile amines, and trimethylamine show the highest degree of correlation with organoleptic judgment, while succinic acid and alcohol show less correlation.

With salted codfish, Bilinski and Fougère (1959) have studied the inhibitory effect of salt on proteolysis of the muscle and deamination of amino acids and formation of trimethylamine. The non-protein nitrogenous constituents were also studied by Freixo (1958) in Portuguese light-salted cod. It has also been

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noted (Cardin *et al.*, 1958) that there is a substantial degree of formation of free fatty acids during processing of salted codfish but it was found to be the same in two types of cures widely different in salt content, namely the light-salted Gaspé cure and the heavy-salted cure. Preliminary determinations also have shown that the amounts of volatile reducing substances do not vary substantially between the light-salted and heavy-salted cure, while on the contrary the total volatile acids content showed significant differences.

In the present investigation the development of the free α-amino acids, ammonia, trimethylamine and volatile acids were examined for their possibilities of defining and of characterizing three different types of salted codfish.

EXPERIMENTAL

Material

The three types of salted cod can be briefly described as follows: the "Gaspé cure" is a light-salted fish cured by adding 8 to 10 lb of salt per 100 lb of fresh fish. It is kept in the brine for 3 days then dried in the sun to 38% moisture content. The "Fall cure", which is also considered as a light-salted cure, is processed by adding 10 to 14 lb of salt per 100 lb of fish. It is kept in pickle during 6 days then dried to 43% moisture content. The "heavy-salt" is prepared by adding 35 lb of salt to 100 lb of fish and keeping them in the brine for a period of at least 21 days. It can be dried to 40% moisture content (van Klaveren and Legendre, 1958).

Fifty codfish of each type of cure have been analyzed. The fish were caught in the Gulf of St. Lawrence and processed by the industry. To obtain more uniform sampling, all the fish analyzed were taken from lots classified by fishery inspectors as "Choice grade". The salted fish was skinned and the thick part only of the flesh along the backbone was minced and used directly for analysis.

Analytical Methods

All the results were calculated on the dry weight of the flesh, salt excluded. The moisture and salt content determinations were done according to conventional methods. Methods used for the other determinations were as follows:

Total volatile acids (TVA): These were steam distilled into 0.02*N* NaOH, according to the method of Friedemann (1938) as modified by Sigurdson (1947).

Trimethylamine (TMA) *and ammonia*: 25 g of heavy-salted cod or 8 g of Gaspé cure or Fall cure were used for the determination. After addition of 200 ml of water, the sample was homogenized for about 1½ minutes in a Waring Blendor fitted with a screw cap. One-ml aliquants of the resulting suspension were used for analysis. Total volatile nitrogen and TMA were estimated by the micro-diffusion technique of Conway and Byrne (1933) as modified by Beatty and Gibbons (1937). Ammonia was calculated from the difference between the total volatile nitrogen and TMA nitrogen.

Total free α-amino acids: The procedure of van Slyke *et al.* (1941) measuring the amount of free α-amino acids by titration of carbon dioxide evolved during the reaction with ninhydrin was slightly modified so that direct determination on salted cod could be possible. A 50-ml instead of 25-ml reaction vessel was used. One gram of material, salt excluded, was employed for the determination and 10 ml of water, 2 g citrate buffer pH 2.5 and 250 mg of ninhydrin were added. The boiling time for the reaction and for the distillation were respectively 10 and 5 minutes. Blank determinations were made on each sample of fish with all the reagents except ninhydrin.

RESULTS AND DISCUSSION

The mean content of salt and decomposition products determined in the three types of cure is given in Table I.

TABLE I. Mean decomposition products and NaCl content for three types of salted codfish. TVA values are expressed in millilitres of 0.01*N* NaOH per gram of fish (dry, NaCl-free weight); TMA, ammonia and free α-amino acids in milligrams nitrogen per gram of dry, NaCl-free fish; NaCl as percentage of dry weight. Between parentheses are the limit values obtained.

Compound	Heavy-salt	Fall cure	Gaspé cure
TVA	1.85	6.49	9.66
TMA	0.31	1.66	1.95
Ammonia	0.88	1.35	1.76
Free α-amino acids	2.01	2.50	2.82
NaCl	35.8 (32.3–41.5)	26.7 (21.0–31.7)	19.6 (16.2–23.9)

It can be seen that the mean value of each decomposition product increases with cure of lower salt content. Moreover the TVA and TMA contents are those which show the greatest differences between the three types of cure. In fact, five times more TVA or TMA occur in light-salted Gaspé cure than in the heavy-salt, while the difference is much smaller for ammonia and even less for α-amino acids. The influence of the salt concentration on the formation of decomposition products will be discussed further, but it can be noted here that the salt content of the fish within the same cure varies widely and that the two light-salted cures have salt contents that overlap considerably. The Fall cure particularly extends from the mean value of the Gaspé cure to the values of heavy-salt.

Figures 1, 2, 3 and 4 show the variation in the content of each decomposition product within each type of cure and equally show the differences between the three types of cure.

In each Figure, on the abscissa the total variation in amount of the decomposition product, for one type of salted cod, is divided into four equal groups and the percentage of samples found in each group can be read on the ordinate.

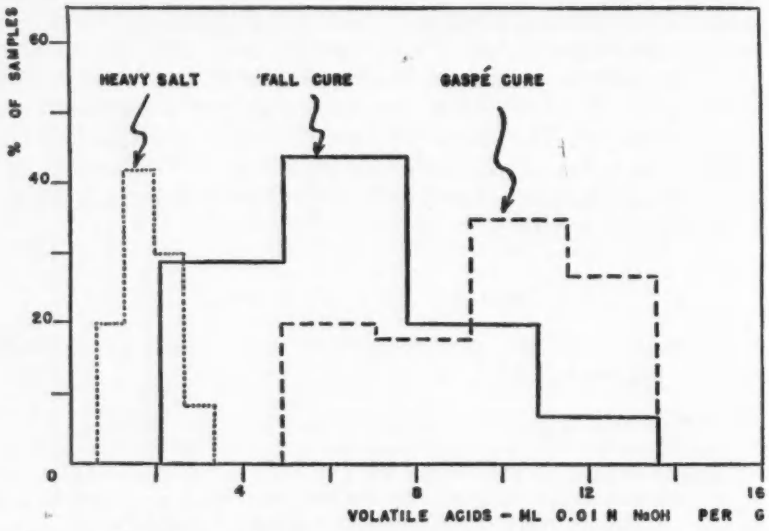

FIG. 1. Distribution of total volatile acids content in three types of salted codfish.

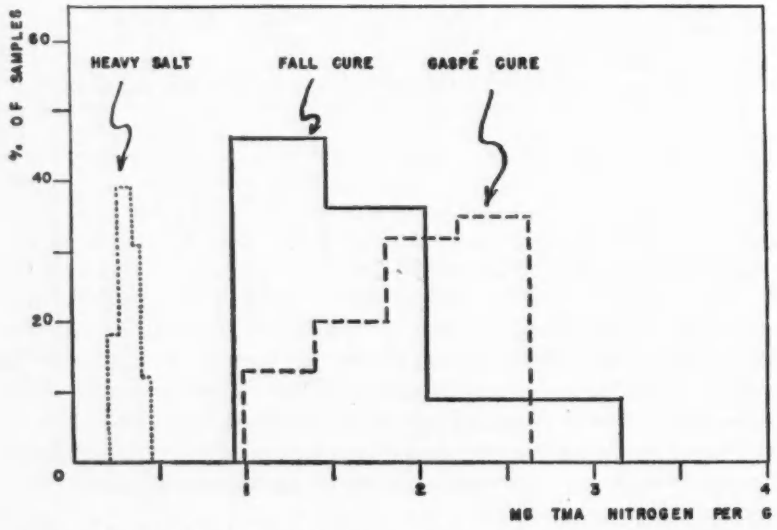

FIG. 2. Distribution of trimethylamine content in three types of salted codfish.

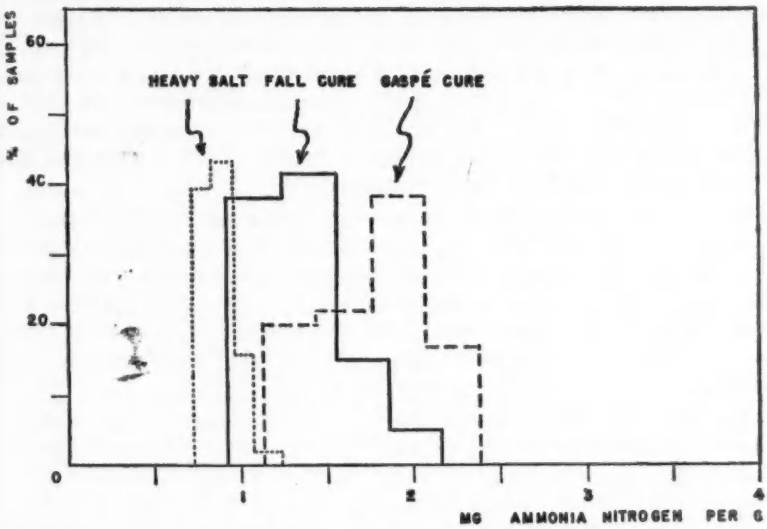

FIG. 3. Distribution of ammonia content in three types of salted codfish.

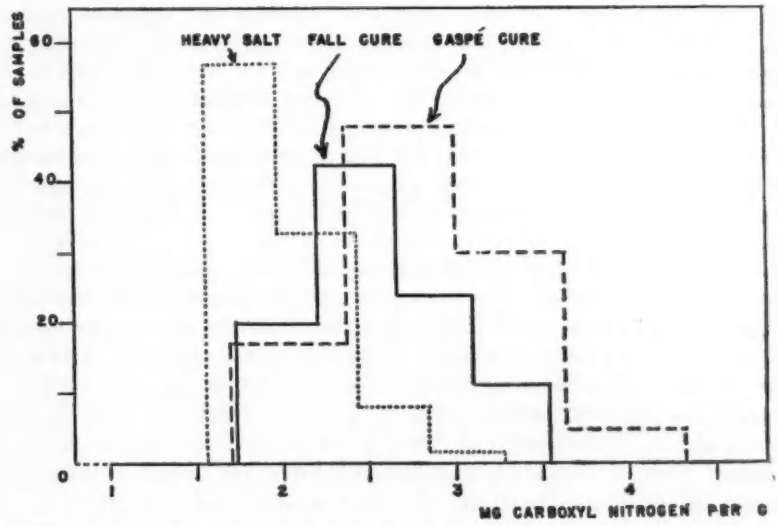

FIG. 4. Distribution of free α-amino acids content in three types of salted codfish.

In Fig. 1, the TVA content is not so widespread in the heavy-salted as in light-salted cures. The distribution of the heavy-salt is clearly separated from that of the Gaspé cure, and the Fall cure occupies an intermediate position. The TMA values (Fig. 2) vary less than the TVA values in the case of heavy-salted cure and are clearly separated from those of both the Gaspé cure and Fall cure. However, in the light-salted cures, the TMA content varies considerably within the same type of cure and the differentiation between the Fall cure and Gaspé cure is less obvious than with the TVA values.

The ammonia content (Fig. 3) is also more homogeneous in the heavy-salted than in the light-salted cures, but the differences already noted between the heavy-salted and light-salted cures are less apparent than for the TVA and TMA. Finally, for the α-amino acids (Fig. 4) there are wide variations within each type of cure even for the heavy-salted cure and, although the mean content in α-amino acids is different for each cure (Table I), it is impossible to see a clear distinction between the different types of salted cod.

The differences observed in the content of decomposition products in light- and heavy-salted codfish must be related with the process of decomposition of the flesh on the one hand and the preservative action of the salt on the other. It is well established with unsalted cod that TMA and TVA contents are indices of decomposition of the flesh (Hillig *et al.*, 1958). On the other hand, the inhibiting action of salt on the formation of TMA in cod has been already noted by Labrie and Gibbons (1937), Winter (1950), Castell and Snow (1951) and Bilinski and Fougère (1959). The formation of quite a large quantity of volatile acids in the Gaspé cure light-salted cod has also been observed by Fougère (personal communication). The present paper, however, brings out the marked difference in TMA and TVA content between commercial types of light-salted and heavy-salted cod. It is apparent that a large formation of TMA and TVA is quite typical of the light-salted cures and especially of the Gaspé cure. The effect of salt on the variation of free amino acids has been studied by Bilinski and Fougère (1959) and it has been observed that a large formation of free amino acids only occurred with small concentrations of salt and when the muscle was well decomposed, and when considerable proteolysis of the muscle has taken place. In the presence of salt, a partial destruction of amino acids with liberation of ammonia could be noticed. With the commercial samples studied in this paper, the quantity of salt added to the fish is sufficient to prevent extensive proteolysis of the flesh and only a limited increase in free amino acids is observed. In a study on Portuguese light-salted cod, Freixo (1958) also found that the amount of decomposition products increases with cures of lower salt content. His data for free amino acids, ammonia and TMA are in the range of those presented in this paper. However the TMA and ammonia content of Portuguese light-salted cures appears to be somewhat lower than that of Gaspé cure and Fall cure.

The better preservation of the flesh from decomposition by employing increasing concentrations of salt can be explained by some observations on the concentration of salt in the flesh of the fish during processing. The concentration

of the brine in the tank, when cod is removed after salting, is 49 to 60% saturated for the light-salted Gaspé-cure, 57 to 78% saturated for the light-salted Fall cure, and 100% saturated for the heavy-salted cure (H. P. Dussault, personal communication). At the same time, the state of saturation of the flesh itself, that is if one takes into account the salt and water content of the flesh, is 86% saturated in the heavy-salted cure, 22 to 35% saturated in the Fall cure and 15 to 22% saturated in the Gaspé cure. Incidentally at this stage of processing, the water content of the flesh is 58% in the heavy-salted cure, 71 to 75% in the Fall cure and 75% in the Gaspé cure. Therefore, whereas the flesh of the heavy-salted cure is continually in the presence of highly concentrated brine which protects the flesh from decomposition, the light-salted fish, while pickling in the brine and even more when it comes out of the brine tank, is highly susceptible to decomposition as the saturation of salt in the flesh is low and its water content is still very high. This might explain the fact that the content of decomposition products is more homogeneous in the heavy-salted than in the light-salted cures. This resemblance in salt saturation between the two light-salted cures might also be the main reason why the content of decomposition products in the dried fish overlaps and is not well separated. Similar observations have been made by Murata and Oishi (1953) who state that "putrefaction in salted fish meat does not occur if the NaCl content becomes 75% of saturated".

It can be concluded from this study that in salted codfish the TMA and TVA contents are chemical indices of decomposition which enable differentiation between light- and heavy-salted cures. The presence of larger quantities of these two decomposition products is typical of light-salted cures, especially Gaspé cure. The ammonia content, and to even less extent the free α-amino acids content, of salted codfish do not show well-marked differences between the light- and heavy-salted cures. The chemical composition of heavy-salted codfish appears to be more homogeneous than the two types of light-salted codfish.

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Effect of Estradiol Monobenzoate on some Serum Constituents of Maturing Sockeye Salmon (*Oncorhynchus nerka*)[1,2]

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ABSTRACT

Blood changes associated with egg production or estrogenization in other egg-laying vertebrates have been obtained in adult sockeye salmon. The blood picture of male salmon following estrogenization approaches that of sexually maturing females. Exogenous estrogen superimposed on endogenous gonadal hormones in maturing female salmon enhances the serum changes associated with egg formation.

INTRODUCTION

In oviparous vertebrates each period of egg production is associated with profound changes in blood chemistry of the female. The serum changes, in teleosts [2, 12, 14], in reptiles [8, 14] and in birds [2, 5, 14, 15, 17, 18], include increased concentrations of certain proteins, lipids, vitamins and minerals which are considered to be related to the mobilization of these compounds for egg formation. Several investigators working with teleosts [1, 26], with amphibians [26], with reptiles [8, 26] and with birds [15, 17, 18, 26] have shown that in addition to the normal puberal changes which, as in the mammal, are related to endocrine activity, similar and even greater increases in these serum constituents result from estrogen treatment of egg-laying vertebrates of either sex or of castrates. The study reported here deals with the effect of estradiol monobenzoate on certain serum constituents in adult sockeye salmon, *Oncorhynchus nerka*, during their spawning migration. It forms a part of the study of the physiology and behaviour of salmon outlined by Brett [3].

MATERIALS AND METHODS

Migrating adult sockeye salmon, which were captured at the Great Central Lake dam on the Stamp River near Alberni, British Columbia, were placed in a transportation tank with iced water at 4°C and supplied with excess oxygen. These fish had left the estuary approximately 3 days previously and normally would have spent 3 months in the lake before spawning. The gonads were

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partially developed at the time of capture, the ovaries corresponding to a rating of 2 on the maturation scale proposed by Davidson and Shostrom [7]. Following transportation to the laboratory at Nanaimo, a distance of 80 miles, 10 fish, 5 of each sex, were arbitrarily placed in each of 2 identical tanks containing 1,100 gallons (5,000 liters) of constantly flowing fresh water.

Twenty-four hours after arrival in the laboratory daily injections of 0.2 mg estradiol monobenzoate in aqueous suspension (B.D.H. oestroform aqueous, 1 mg/ml) were begun on each fish in one tank. At the same time each fish in the second tank received 0.2 ml of the hormone suspending medium (stated by the manufacturers to be "an aqueous solution of a methyl cellulose derivative containing a small percentage of a non-ionic wetting agent"). Hypothermia, 2–4°C, was used as anaesthesia during the injections which were $1\frac{1}{4}$ inches deep into the epaxial muscles immediately behind the head.

Twenty-four hours after the fourth injection each fish was bled by amputating the tail and the blood was collected in 50 ml plastic centrifuge tubes. Aliquots of whole blood were transferred immediately to heparinized Wintrobe hematocrit tubes and the balance of the blood was allowed to clot at room temperature. The clots were allowed to contract for 2 hours at 5°C after which the serum samples were obtained by centrifuging at 3°C.

Hematocrit values were obtained by centrifuging at 1,700 g and 3°C for 30 minutes; calcium was determined by the method of Clark and Collip [4], and total protein by the biuret reaction [28]. Phosphoprotein phosphorous was determined by Schneider's [21] procedure. The method of Folch *et al.* [10] employing sodium chloride was used to isolate and purify the lipids which were then stored in hexane at −25°C under nitrogen. Total lipid was determined by drying aliquots of the lipid solution at 100°C. Ten volumes of acetone were added to one volume of lipid solution and the phospholipids allowed to precipitate overnight at −25°C; following centrifugation total neutral lipid was determined by drying aliquots of the supernatant at 100°C. Total and free cholesterol were determined by the procedure of Sperry and Webb [24] and esterified cholesterol by difference. King's [13] method was used to determine protein and lipid phosphorus.

Data were subjected to an overall analysis of variance according to Snedecor [23], and values of the average within group standard deviation are tabulated. Tests were made for effects of injections, for differences between sexes, and for interaction between these two.

RESULTS AND DISCUSSION

The experimental results which are summarized in Table I are discussed separately, but throughout the discussion it must be remembered that the fish were not in reproductive rest during the period of this experiment. The experimental fish were already under the influence of endogenous gonadal hormones which probably influenced the response to exogenous estrogen.

TABLE I. Effect of 4 daily injections of estradiol monobenzoate on some serum constituents of maturing sockeye salmon. Data are averages for 5 fish of each sex on each treatment, and the average within-group standard deviation is shown. Samples were taken 24 hours after last injection. LSD = least significant difference between any two groups. * = significant at P = 0.05. ** = significant at P = 0.01. NS = non-significant (P > 0.05).

	Control		Injected		Common standard deviation	LSD		Tests of significance		
	Male	Female	Male	Female		P = 0.05	P = 0.01	Male vs. female	Control vs. estrogenized	Interaction
Estradiol monobenzoate, *mg*	Nil	Nil	4 × 0.2	4 × 0.2	...	...	...	...	...	...
Body weight, *g*	2205	2074	1995	2060	365	...	...	NS	NS	NS
Testes weight, *g*	16.9	...	16.6	...	8.89	...	...	...	NS	...
Ovary weight, *g*	...	93.7	...	94.0	13.7	...	...	...	NS	...
Testes wt./body wt. × 10^3	7	...	8	...	...	...	...	...	NS	...
Ovary wt./body wt. × 10^3	...	43	...	45	...	...	...	...	NS	...
Egg diameter, *mm*	...	2.5	...	2.6	...	...	...	...	NS	...
Hematocrit value, *%*	48	47	39	41	2.63	3.5	4.8	NS	**	NS
Calcium, *mg/100 ml*	11.8	13.1	15.1	17.6	1.13	1.3	1.7	*	**	NS
Total protein, *g/100 ml*	4.8	5.1	5.2	6.0	0.41	0.6	0.9	*	**	NS
Total lipid, *g/100 ml*	2.4	2.0	4.6	5.0	0.90	1.2	1.6	NS	**	NS
Neutral lipid, *g/100 ml*	1.9	1.7	3.9	4.1	0.75	1.0	1.4	NS	**	NS
Total cholesterol, *g/100 ml*	0.36	0.24	0.45	0.50	0.09	0.12	0.16	NS	**	*
Free cholesterol, *g/100 ml*	0.12	0.09	0.22	0.26	0.04	0.06	0.08	NS	**	NS
Cholesterol ester, *g/100 ml*	0.24	0.15	0.23	0.24	0.07	...	...	NS	NS	NS
Protein phosphorus, *mg/100 ml*	3.0	7.4	8.7	13.5	0.98	1.3	1.8	**	**	NS
Lipid phosphorus, *mg/100 ml*	57.0	43.1	81.5	97.4	26.4	35.2	48.7	NS	**	NS

Body Weight, Gonad Weight and Egg Diameter

There was no significant difference in total body weight between the four groups of fish, and estrogenization had no effect on gonad weight, ratio of gonad weight to total body weight or egg diameter.

Hematocrit

Despite differences in hematocrit values between control and estrogenized animals, there was no significant difference between control male and female salmon or between estrogenized males and females. From previous work with mammals [11], with birds [9, 19] and with the killifish (*Fundulus heteroclitus*) [22], maturing male salmon would be expected to have higher hematocrit values than maturing females. However, Lysaia [16] has reported that maturing male pink salmon captured in an estuary had a lower red cell count than females in one particular year but a higher count than females in the following year.

Estrogenization resulted in a highly significant decrease in the hematocrit values of both male and female salmon. Since excessive estrogens may cause a positive electrolyte and water balance in mammals [11] the decreased hematocrit values reported here for salmon may be due to hemodilution. Conflicting results have been reported on the effects of estrogens in birds. Thus Domm and Taber [9] demonstrated that large doses of estrogen resulted in a diminution in red blood cell count of castrate female chickens, whereas Sturkie [25] states that estrogen has no effect on the hematocrit of chickens.

Calcium and Protein Phosphorus

It has been demonstrated repeatedly that in all classes of egg-laying vertebrates the levels of serum calcium and protein phosphorus are increased during egg formation or following estrogenization. McDonald and Riddle [17] working with pigeons, and Bailey [1] working with goldfish, have found a correlation between the increased levels of certain calcium fractions and protein phosphorus. Schjeide and Urist [20] have reported that practically all of the serum calcium in estrogenized roosters may be complexed with phosphoprotein, lipoprotein and albumin. However, it has been shown [27] that liver synthesis is the only source of serum phosphoprotein in estrogenized cockerels, and that in functionally hepatectomized estrogenized cockerels there was no correlation between the levels of plasma calcium and protein phosphorus. The present experiment shows that, as in other oviparous vertebrates with intact livers, maturing female salmon have higher serum calcium and protein phosphorus levels than males, and that the levels of both these constituents are increased by exogenous estrogen.

Total Protein and Lipid Constituents

There was no significant difference in the serum levels of total protein, total lipid, neutral lipid, total cholesterol, free cholesterol, esterified cholesterol and lipid phosphorus between control male and female salmon. However, estrogen

increased the levels of all these constituents with the exception of esterified cholesterol. The lack of increased levels in the control females which were under the influence of endogenous estrogen may be attributed to the fact that these are yolk constituents and were probably being utilized by the developing ova at the same rate that they were being produced from body stores. These constituents can not be utilized by the male in the same manner and therefore accumulate in the blood following estrogenization. A similar accumulation in the female following estrogenization may be due to an excess production of these constituents or may in part be a reflection of decreased ovum growth since it has been found [6] that estrogen causes some regression or inhibition of growth of the quiescent ovary of prepuberal pullets.

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Fatty Alcohols from Marine Oils and Segregated Esters[1]

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ABSTRACT

Fatty alcohols were prepared by lithium aluminium hydride reduction of the three main methyl ester fractions obtained by countercurrent extraction of methyl esters from herring oil.

Alcohols were also prepared by the same method from commercially important Canadian marine oils, e.g. cod oil, cod liver oil, seal oil, herring oil and dogfish liver oil, and their properties tabulated.

A comparison was made between the sodium reduction method and the lithium aluminium hydride method in the reduction of methyl esters from herring oil and their effect on producing conjugation of the ethylenic double bonds.

INTRODUCTION

In earlier reports from this laboratory (Vandenheuvel and Jangaard, 1957; Jangaard and Vandenheuvel, 1961a) a procedure for continuously producing from marine oils fatty acid methyl esters having specific properties was described. The following components comprise the three fractions obtained from herring oil: fraction I, methyl esters of $C_{14} - C_{16}$ acids; fraction II, esters of $C_{18} - C_{20} - C_{22}$ mono-unsaturated acids; fraction III, esters of $C_{18} - C_{20} - C_{22}$ highly unsaturated acids.

Since any of these varied types of fatty acids may be found randomly arranged in a glyceride molecule in the original oil, no sharp segregation can be obtained using the whole oil. By varying the extraction temperature, flow, and ratio of methyl esters to solvent (nitromethane) the iodine value and composition of the three fractions produced from the corresponding methyl esters can be changed to meet specifications. It was thought that these fractions when converted to alcohols would be of more general interest than alcohols prepared from the whole oil, especially the unique highly unsaturated fraction.

Several workers have reported reducing marine oils to alcohols using the sodium reduction method. Hansley (1947) prepared alcohols from menhaden oil and cod liver oil and Pryde (1951) reported that the recovered menhaden oil alcohols contained 15 to 20% alcohols with conjugated double bonds. Hill *et al.* (1954) lists the alcohols prepared from sardine and menhaden oil and Gruger (1957a) used menhaden and pilchard oil as starting material. Gruger tried fractional distillation, urea inclusion products, and crystallization to fractionate the products.

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To our knowledge, no publications have described the properties of alcohols prepared from marine oils using the lithium aluminium hydride method, although Gruger (1957b) pointed out the advantages of this method.

The increased interest in fatty alcohols can be appreciated from the fact that the production in the United States quadrupled in the four years from 1954 to 1958 (Manufacturing Chemists' Assoc., Inc., 1960). This reflects the growth of synthetic detergents in that period, since these represent the largest market for fatty alcohols. Of the earlier detergents, the ones based on lauryl alcohol prepared from cocoanut oil were most common. However, with new processes and raw materials available, a wide variety of fats is used for alcohol production and detergents with superior properties for many specialty uses may be compounded from them (Hill *et al.*, 1954).

The two principal processes currently in use industrially are the sodium reduction method and hydrogenolysis. In addition a laboratory method utilizing lithium aluminium hydride is available. In all these processes it is economically advantageous to first convert glycerides to simpler (e.g. methyl) esters of the fatty acids because of the ease of recovery of high-purity glycerol in good yield from the simple alcoholysis reaction (Jangaard and Vandenheuvel, 1961b). In hydrogenolysis the glycerol would be reduced to propylene glycol and 2-propanol if triglycerides were used as raw material and in the sodium reduction process glycerol would have to be recovered from a caustic solution.

In hydrogenolysis, fatty acids, anhydrides, esters or salts are converted to fatty alcohols by contact with hydrogen at high temperatures (200 to 350°C) and pressures (100 to 200 atmospheres) in the presence of a catalyst according to the following equation:

$$RCOOH + 2H_2 \rightarrow RCH_2OH + H_2O$$

Under these conditions and with the catalysts commonly used (e.g. copper chromite) the double bonds are hydrogenated to give saturated alcohols. More recently it had been claimed that by using larger amounts of catalyst and by adding cadmium salts, the double bonds may be partially or wholly protected and unsaturated alcohols produced (Martinez Moreno *et al.*, 1959). Numerous patents on the process have been granted in the last two decades.

The sodium reduction method makes possible the convenient production of unsaturated as well as saturated alcohols. The procedure is basically the method of Bouveault and Blanc (1903) as modified by Hansley (1947). The overall reaction can be summarized as follows:

$$RCOOR' + 4Na + 2R''OH \rightarrow RCH_2ONa + R'ONa + 2R''ONa$$

$$RCH_2ONa + R'ONa + 2R''ONa + 4H_2O \rightarrow RCH_2OH + R'OH + 2R''OH + 4NaOH$$

The reaction is carried out at atmospheric pressure and consists of adding a solution of dry and neutral ester, reducing alcohol (e.g. methyl isobutyl carbinol) and solvent, usually xylene, to a stirred dispersion of sodium in xylene. The reaction is rapid and exothermic and is controlled by condensing the refluxing

xylene. The unreacted sodium is destroyed with steam, which also decomposes the complex and liberates the alcohols.

Recovery of reducing alcohol and solvent is simplified if the esters are derived from the reducing alcohol, for example fatty acid methyl isobutyl carbinol esters which can be prepared by alcoholysis from the triglycerides (Hill *et al.*, 1954).

A laboratory method for reduction of acids and esters, first described by Nystrom and Brown (1947), employs lithium aluminium hydride ($LiAlH_4$) in ether solution at room temperature. The excess $LiAlH_4$ is decomposed with dilute acid and the alcohols are recovered from the ether solution. No appreciable conjugation of the double bonds occurs at these low temperatures and this method is therefore the only one available to produce alcohols from marine oils with the carbon-to-carbon unsaturation unchanged. The reaction can be summarized as follows:

$$2RCOOR' + LiAlH_4 \rightarrow LiAl(OCH_2R)_2(OR')_2 \xrightarrow{H_2O} 2RCH_2OH + 2R'OH.$$

EXPERIMENTAL

Sodium Reduction

Sodium (15.4 g) and freshly dried xylene (53 ml) were placed in a 1-litre 3-necked flask equipped with a stirrer driven by a powerful air motor. The flask was fitted with a dropping funnel and reflux condenser with drying tube and heated by an electric mantle. The sodium was melted and finely dispersed with rapid stirring. Methyl esters (50 g) and methyl isobutyl carbinol (42 ml) in xylene (150 ml) were added from a dropping funnel, the heat of reaction being removed by refluxing. By using these large amounts of solvent the reaction was easily controlled and the danger of gelling was diminished. The addition was completed in 15 to 20 min and the refluxing and stirring were continued for another 40 min.

The reaction mixture was then hydrolyzed by introducing small amounts from a dropping funnel into a hydrolysis flask where the mixture was kept boiling the admission of steam. The excess sodium decomposed smoothly, and the xylene + methyl isobutyl carbinol was removed by the steam distillation. The organic layer separating in the flask was washed with brine, and the alcohols were distilled under vacuum. The soaps remained in the residue.

Difficulties with gelling due to soap formation will be encountered if (1) the starting material contains an appreciable amount of free fatty acids, and (2) the solvents, esters, and apparatus have not been thoroughly dried and protected against moisture.

In a case when the reaction mixture had gelled and could not be dropped into the hydrolysis flask, the excess sodium was decomposed with anhydrous methanol (500 ml, somewhat more than necessary to dissolve the gel). Water (300 ml) was added to decompose the complex and the mixture was shaken in a separatory funnel. Petroleum ether (250 ml) was then added, and the fatty alcohol + petroleum ether + xylene + methyl isobutyl carbinol layer was washed with water. The solvents were then removed under vacuum and the

alcohols vacuum-distilled. By using this procedure the amount of conjugation of the double bonds was found to be considerably reduced.

The yields in both cases were about 85% of the theoretical.

Lithium Aluminium Hydride Reduction

Reagent ethyl ether was dried by distillation over $LiAlH_4$, then 30 g $LiAlH_4$ was added to 1000 ml of the distillate and refluxed for 6 hours. The solution was stored in 100-ml bottles with polyethylene-lined caps.

One hundred millilitres of the solution containing approximately 3 g $LiAlH_4$ was added to dried ether (50 ml) in a 1000-ml 4-necked flask under a stream of nitrogen. The flask was equipped with a stirrer, a reflux condenser and a dropping funnel.

Thirty grams of oil or methyl esters was dissolved in 100 ml anhydrous ether and added from the dropping funnel with rapid stirring over a period of approximately 20 min and the reaction mixture was refluxed for another 30 min. After cooling it in an ice bath, 30 ml of 10% H_2SO_4 and 50 ml water were added slowly to decompose the excess $LiAlH_4$. Efficient stirring is essential at this point to break any gel that may form. The acidified mixture was transferred to a separatory funnel and the water layer extracted with ether. The ether layer was washed with water until neutral to litmus, dried over sodium sulphate and the ether evaporated. The alcohols were then vacuum-distilled. The yields were of the order of 95 to 99% of the theoretical.

The saponification value, iodine value, free fatty acids and unsaponifiable matter of all products were determined according to the American Oil Chemists' Society Official Methods (1946).

The hydroxyl values were determined using Verbeck's pyridine–phthalic anhydride method (1947). The ultraviolet absorption spectra for conjugated constituents were determined in *iso*-octane with a Beckman DK-2 spectrophotometer.

The gas chromatographic analyses of the acetylated alcohols (Link *et al.*, 1959) were performed on a Wilkins Aerograph, column packing DEGS polyester substrate, 25% on Chromosorb, column dimensions $\frac{1}{4}$ inch by 10 feet (6 mm by 3 m), oven temperature 210°C.

RESULTS AND DISCUSSION

Table I lists the physical constants of methyl esters from whole herring oil and of the three ester fractions obtained by countercurrent segregation using

Table I. Physical constants of methyl esters.

	Iodine value	Refractive index at 25°C	Saponification value	Free fatty acids	Unsaponifiable matter	Av. mol. wt. of fatty acids from sap. value
				%	%	
Methyl esters from herring oil	134.5	1.45645	189.0	0.05	0.9	284
Segregated methyl esters:						
Fraction I	39.8	1.44250	208.7	0.6	<0.1	256
Fraction II	117.9	1.45670	180.6	0.3	<0.1	297
Fraction III	233.8	1.46930	185.7	0.7	<0.1	290

nitromethane; Table II gives the constants for the fatty alcohols produced by $LiAlH_4$ reduction of these esters.

TABLE II. Physical constants of alcohols reduced from methyl esters using lithium aluminium hydride.

Alcohols from	Iodine value	Refractive index at 25°C	Distilling range at 0.2 mm	Hydroxyl value	Hydroxyl (OH)	Free fatty acids	Saponification value	Av. mol. wt. from OH value
			°C		%	%		
Methyl esters from herring oil	146.0	1.46443	120–170	207.6	6.29	0.04	0.6	270
Segregated methyl esters:								
Fraction I	43.9	(solid)	118–138	229.7	6.96	0.06	0.6	244
Fraction II	132.7	1.46500	136–170	198.1	6.00	0.09	0.8	283
Fraction III	255.9	1.47810	130–174	199.7	6.05	0.08	1.0	280

Figure 1 gives the gas chromatographic analysis of acetylated alcohols prepared from three fractions with tentative identification of some of the major component peaks.

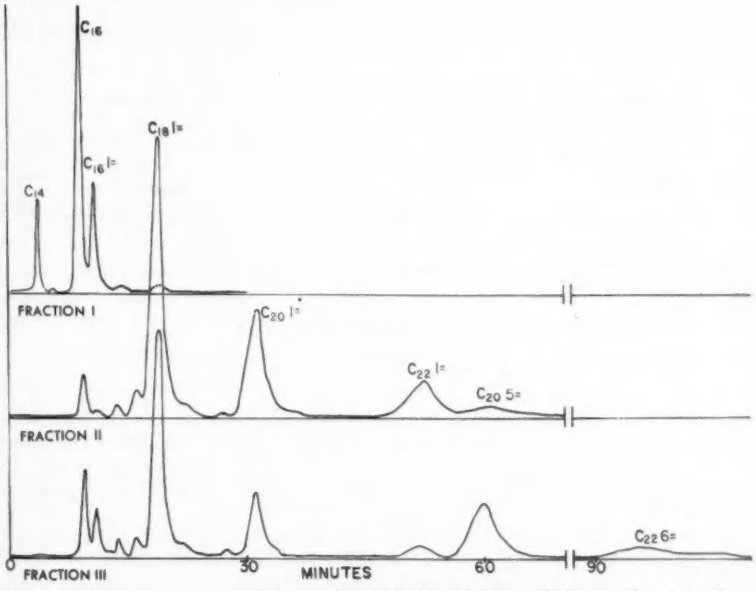

FIG. 1. Gas chromatograms of acetylated alcohols from methyl ester fractions from herring oil, with tentative identification of some of the peaks. Sample size I: 0.001 ml; II and III: 0.004 ml.

Fraction I alcohol is a white solid at room temperature and contains mainly $C_{14} - C_{16}$ saturated alcohols with smaller amounts of $C_{14} - C_{16} - C_{18}$ alcohols with one double bond.

Fraction II is a colourless, oily liquid with a slight odour. It contains a high percentage of the mono-unsaturated alcohols of the $C_{18} - C_{20} - C_{22}$ series, but also

a small amount of those of higher unsaturation. A slight selective hydrogenation to an iodine value of 90 to 100 from the original 133 should give a fraction containing 70 to 80% mono-unsaturated $C_{18} - C_{20} - C_{22}$, the remainder being saturated and diene alcohols.

Fractions I and II are similar to alcohols obtained from vegetable and animal fats, and are used in the production of detergents, cosmetics, lubricant additives, defoamers and chemical intermediates. However, fraction III is unique and contains most of the highly unsaturated alcohols with 3, 4, 5 and 6 double bonds typical of the marine oils. It is a pale yellow oily liquid with a "fishy" odour. Because of its high unsaturation, it should be of interest as a chemical intermediate in protective coatings, organic synthesis and surfactant manufacture and also in pharmaceutical applications.

In Table III the physical constants of some commercially important marine oils of Canadian origin are given and in Table IV the constants of the alcohols prepared from them by $LiAlH_4$ reduction. All these alcohols are colourless to straw-coloured, slightly viscous liquids with slight "fishy" odours. However, in most cases the odours are much milder and less offensive in the alcohols than in the starting material.

TABLE III. Physical constants of marine oils used for reduction.

Type of oil	Iodine value	Refractive index at 25°C	Saponification value	Free fatty acids	Unsaponifiable matter
				%	%
Cod oil, sunrotted, Newfoundland	168.9	1.47678	187.5	10.5	1.3
Cod liver oil, Newfoundland	170.3	1.47780	185.4	0.8	1.5
Cod liver oil, solvent-extracted in laboratory	182.7	1.47919	182.7	0.5	1.2
Herring oil, British Columbia	136.9	1.47360	189.6	1.1	1.0
Seal oil, harp seal	149.7	1.47478	192.0	0.7	0.3
Dogfish liver oil, British Columbia	117.2	1.47165	161.3	1.2	15.6

TABLE IV. Physical constants of fatty alcohols, lithium aluminium hydride reduction.

Alcohols from	Iodine value	Refractive index at 25°C	Distilling range at 0.2 mm	Hydroxyl value	Hydroxyl (OH)	Saponification value	Free fatty acids	Av. mol. wt. from OH value
			°C		%		%	%
Cod oil, sunrotted, Nfld.	180.5	1.46852	116–165	196.4	5.95	0.37	0.11	286
Cod liver oil, Nfld.	182.0	1.46866	116–162	198.1	6.00	0.73	0.06	283
Cod liver oil, solvent-extracted in laboratory	197.5	1.47040	120–167	199.4	6.04	0.73	0.09	282
Herring oil, B.C.	146.5	1.46458	120–175	204.6	6.20	0.09	0.10	274
Seal oil, harp seal	161.9	1.46620	122–167	204.9	6.21	2.09	0.16	274
Dogfish liver oil, B.C.	124.0	1.46357	120–174	211.9	6.42	0.63	0.11	265

To compare the two commonly used laboratory methods, sodium and $LiAlH_4$ reductions, a few sodium reductions were performed on the methyl esters from herring oil. In one of the experiments the reaction mass was added to boiling water and the solvents were steam distilled as recommended by Hansley. In a second experiment, the excess sodium was decomposed with anhydrous methanol as described above. Much less conjugation of the double bonds was found in the

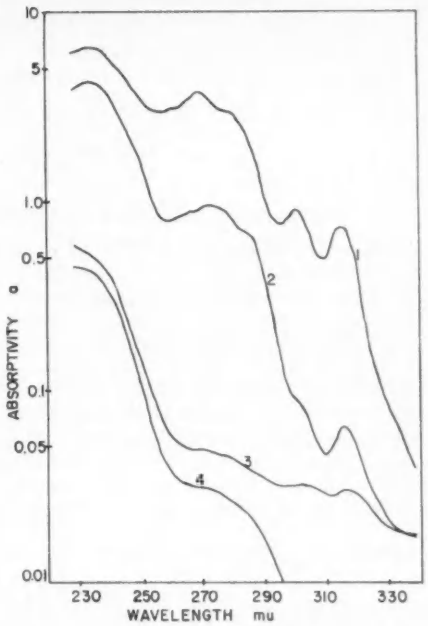

FIG. 2. Conjugation of double bonds in alcohols reduced from methyl esters from herring oil.

1. Sodium reduction, excess sodium decomposed with steam.
2. Sodium reduction, excess sodium decomposed with methanol.
3. Methyl esters.
4. Lithium aluminium hydride reduction.

alcohols prepared by the latter method, indicating that most of the conjugation takes place in the steam hydrolysis and distillation step, as well as in the reduction proper. Figure 2 shows the ultraviolet absorption curves of these samples (in *iso*-octane), of the alcohols prepared by the $LiAlH_4$ method, and also of the original methyl esters. In the $LiAlH_4$ method there is actually a slight lessening in the amount of conjugation, due probably to the reduction of peroxides and other materials.

An attempt was made to calculate the actual percentage of conjugated constituents using the formulas given in A.O.C.S. Official Methods for glycerides, esters, and fatty acids. No formulas are given for fatty alcohols, so the values can only be approximate. The results are summarized in Table V.

TABLE V. Total conjugated constituents in methyl esters and alcohols.

Type of bond	Original methyl esters from herring oil		Alcohols					
			Sodium-reduced steam distilled		Sodium-reduced methanol added		$LiAlH_4$-reduced	
	A*	C*	A	C	A	C	A	C
		%		%		%		%
Conjugated diene	0.5	0.45	6.5	5.9	4.3	3.9	0.4	0.36
Conjugated triene	...	...	1.76	0.083	0.28	0.13	...	...
Conjugated tetraene	...	...	0.85	0.38	0.02	0.01	...	...
Conjugated pentaene	...	...	...	trace	...	...	...	...
Total conjugated material	–	0.45	–	7.11	–	4.04	–	0.36

*A = absorptivity; C = conjugated alcohols.

The data in Table V show that a decrease of conjugation to almost one-half can be achieved by eliminating or shortening the steam treatment of the reaction mass. Even so, the total conjugation with the sodium reduction method is more than ten times as high as in the alcohols prepared by $LiAlH_4$ reduction.

SUMMARY

The properties of fatty alcohols from fatty-acid methyl ester fractions from herring oil and several commercially important marine oils are tabulated.

Some decrease in the conjugation using the sodium reduction method could be effected by decomposing the excess sodium with methanol and vacuum-distilling the solvents, as compared to the water quenching and steam distillation procedure in use commercially.

The lithium aluminium hydride reduction method is the only procedure whereby fatty alcohols can be prepared from marine oils without some changes in the ethylenic double bonds taking place.

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Growth and Age Determination of the Pacific Edible Crab *Cancer magister* Dana[1]

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ABSTRACT

Of 2,820 early post-larval unsexed crabs collected by small-meshed trawl in two regions of the Queen Charlotte Islands, 1,175 were measured and the 1st and 2nd post-larval instars were identified as modes at 6.9 and 10.0 mm, respectively. Increments of 5 unsexed moulted crabs, carapace widths 6.80 to 9.96 mm, were from 36.3 to 46.5%. A total of 284 males, from 83 to 186 mm, moulted in crab traps, live-wells, and while at large as tagged specimens; 44 females, from 88 to 145 mm, moulted in traps. Using equations of regression of new carapace width on old width for both sexes and starting at the 2nd instar, average carapace widths were calculated for instars 3 to 15. In the width-frequency distributions of 8,145 crabs, separation of stages was sufficient for identification of age-groups. It is estimated that a year after hatching, males reach stage 5 or 6 (24.2 or 31.1 mm); after 2 years stage 11 or 12 (96.6 or 119.5 mm) is attained; after 3 years stage 13 (146.9 mm); after 4 years most males are in the 14th stage (176.2 mm) and above the British Columbia legal size of 165 mm; and generally after 5 years males are in stage 15 (207.5 mm). Growth of females is similar for 2 years, but afterwards is slower.

INTRODUCTION

The first study of the growth of the Pacific edible crab, *Cancer magister*, was conducted by MacKay and Weymouth (1935). On the basis of measurements and moulting records of crabs from Boundary Bay in southern British Columbia, they were able to determine growth rate and estimate age. Male crabs were found to pass through 17 post-larval instars, attaining maturity at 4 or 5 years, and reaching the British Columbia legal size, 6½ inches or 165 mm in carapace width, after 7 or 8 years. Sixteen instars were required for maturity of females, which mature at about the same age as males but rarely reach legal size.

Cleaver (1949), using moulting records and measurements from the coast of Washington, found a more rapid growth than MacKay and Weymouth. Most individuals of both sexes attained maturity after 3 years; and males had reached legal size (169 mm in Washington) in the 14th or 15th instar, after 4 years. Growth of females for the first 2 years was similar but subsequently the rate was uncertain.

From 1949 to 1957, as part of a crab investigation in the Queen Charlotte Islands, British Columbia, the writer has attempted to determine growth and age.

SAMPLING OF EARLY POST-LARVAL CRABS

The reproductive cycle of the edible crab in the Queen Charlotte Islands has been described (Butler, 1956). Breeding occurs during the summer; fertilized ova are extruded by the female in early autumn and are carried until hatching in the spring, about April. The larval life lasts about 4 months. The megalops

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is found during August, and metamorphosis into the first post-larval stage occurs during September.

From 1953 to 1956 early post-larval crabs were collected in Naden Harbour and McIntyre Bay, off the north coast of Graham Island. Most sampling was carried out with a small trawl having a beam 80 inches (2.03m) long and constructed of cotton netting of ½-inch stretched mesh. Tows were made during daylight hours and lasted 10 minutes. Crabs were taken most abundantly on sand bottom in inshore regions shallower than 10 fathoms (18 m) (Fig. 1); 2,820 post-larval crabs were taken in 143 tows.

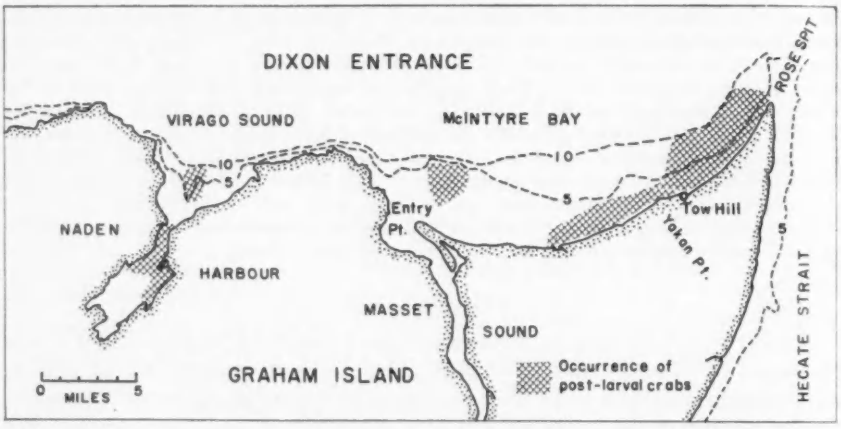

FIG. 1. Map showing the distribution of early post-larval crabs in Naden Harbour and McIntyre Bay, 1953 to 1956. Depths in fathoms.

MOULTING OF POST-LARVAL CRABS. Of about a dozen post-larval crabs which were placed in bottles of sea water immediately after capture, 5 moulted successfully. Four individuals passed from the 1st into the 2nd post-larval stage, and the other from the 2nd into the 3rd stage. Measurements of the carapace width, including the 10th antero-lateral spines, were made with vernier calipers which were accurate to 0.02 mm (Table I). No attempt was made to determine sex of these early stages.

TABLE I. Increase in size of post-larval crabs at moulting.

Instar	Carapace width		Increase	
	Old	New		
	mm	mm	mm	%
1	6.80	9.96	3.16	46.5
1	6.56	9.44	2.88	43.9
1	6.76	9.86	3.10	45.9
1	6.40	8.72	2.32	36.3
Av.	6.63	9.50	2.87	43.2
2	9.96	14.04	4.08	41.0

MEASUREMENT OF EARLY POST-LARVAL STAGES. A sample of 1,175 post-larval crabs, collected in McIntyre Bay from August 29 to September 9, 1953, were measured with vernier calipers. Measurements were rounded to the nearest 0.1 mm, and are plotted in Fig. 2.

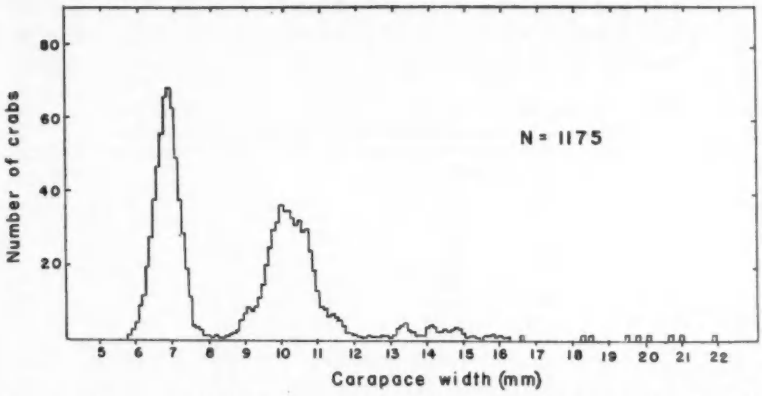

FIG. 2. Carapace width frequency distribution of unsexed post-larval crabs collected in McIntyre Bay, September, 1953.

First post-larval stage crabs range from 5.8 to 8.0 mm, with the mode at 6.9 mm. Carapace widths of the 2nd stage are from 8.2 to about 12.5 mm, and the mode appears at 10.0 mm. Individuals between 13 and 16 mm presumably belong to the 3rd stage, and the remainder in the distribution between 18 and 22 mm are likely 4th stage crabs.

GROWTH PER MOULT OF LARGER CRABS

Moulting records were obtained from several sources. Crabs moult in crab traps and since it is possible to match soft-shelled individuals with their cast-off exoskeletons, increments were determined. Specimens were taken from traps and placed in live-wells where ecdysis occurred within a day or two. Male crabs were marked with a type of tag retained through moulting (Butler, 1957). Some recovered individuals moulted once during their periods of freedom, enabling increments to be determined. A total of 284 male and 44 female records was obtained, as follows:

	Males	*Females*
Moulted in traps	250	44
Moulted in live-wells	22	...
Tag recoveries	12	...

All crabs moulting in traps and live-wells were caught on fishing grounds in Hecate Strait and McIntyre Bay between 1953 and 1957. Of 12 moulted tagged crabs recovered in 1956, 1957, and 1959, 11 were taken in the above two areas, and the other in Naden Harbour. Male moulting records were all considered together, as there were no apparent differences according to locality.

Carapace widths before moulting of all but one male were from 83 to 186 mm; the other was 29 mm. Records were grouped by 5-mm intervals and are summarized in Table II. Absolute and percentage increments are graphed in Fig. 3. Moulting records of females, from 88 to 145 mm, are summarized in Table III. Over this size range, the increments decrease from 24 to 16 mm, or from 27.3% to 11%. Thus, absolute increase per moult of males larger than 90 mm increases with size, whereas successive increments of the females decrease.

TABLE II. Average carapace widths, absolute increments, and percentage increments, for male crabs; also the range of new-shell widths, and of increments.

Size	Crabs	Carapace width		Increment		Ranges	
		Old	New			Width	Increment
mm	*No.*	*mm*	*mm*	*mm*	*%*	*mm*	*mm*
	1	29.0	37.0	8.0	27.6	...	...
80–84	1	83.0	107.0	24.0	28.9	...	...
85–89	3	88.7	113.0	24.3	27.4	110–115	21–26
90–94	2	92.0	117.0	25.0	27.2	115–119	23–27
95–99	6	97.5	123.5	26.0	26.7	121–125	24–28
100–104	2	101.5	124.5	23.0	22.7	124–125	21–25
105–109	3	106.0	133.7	27.7	26.1	131–135	26–30
110–114	3	111.0	137.3	26.3	23.7	133–141	22–29
115–119	3	116.3	144.0	27.7	23.8	140–149	25–30
120–124	2	122.0	149.0	27.0	22.1	144–154	24–30
125–129	7	128.3	156.7	28.4	22.1	153–159	24–31
130–134	15	131.7	160.2	28.5	21.6	154–165	23–31
135–139	11	136.6	165.7	29.1	21.3	162–172	27–34
140–144	22	142.1	172.4	30.3	21.3	164–179	23–35
145–149	32	146.5	177.4	30.9	21.1	171–182	25–35
150–154	43	151.9	182.2	30.3	19.9	168–189	17–36
155–159	53	157.0	186.5	29.5	18.8	174–192	16–35
160–164	44	162.1	191.5	29.4	18.1	170–199	10–35
165–169	15	167.2	197.2	30.0	17.9	189–206	22–38
170–174	6	172.2	199.3	27.1	15.7	195–203	22–31
175–179	5	176.2	208.8	32.6	18.5	203–213	28–35
180–184	4	181.8	211.5	29.7	16.3	208–216	25–35
185–189	1	186.0	218.0	32.0	17.2	...	...

TABLE III. Average carapace widths, absolute increments, and percentage increments, for female crabs; also the range of new-shell widths, and of increments.

Size	Crabs	Carapace width		Increment		Ranges	
		Old	New			Width	Increment
mm	*No.*	*mm*	*mm*	*mm*	*%*	*mm*	*mm*
85–89	1	88.0	112.0	24.0	27.3	...	...
90–94	1	93.0	113.0	20.0	21.5	...	...
95–99	1	99.0	123.0	24.0	24.2	...	...
100–104	1	100.0	117.0	17.0	17.0	...	...
115–119	1	117.0	136.0	19.0	16.2	...	...
125–129	12	127.0	145.1	18.1	14.3	136–149	11–22
130–134	11	132.4	149.8	17.4	13.1	146–152	15–20
135–139	10	137.2	153.9	16.7	12.2	148–158	13–21
140–144	5	141.6	158.2	16.6	11.7	155–161	15–19
145–149	1	145.0	161.0	16.0	11.0	...	...

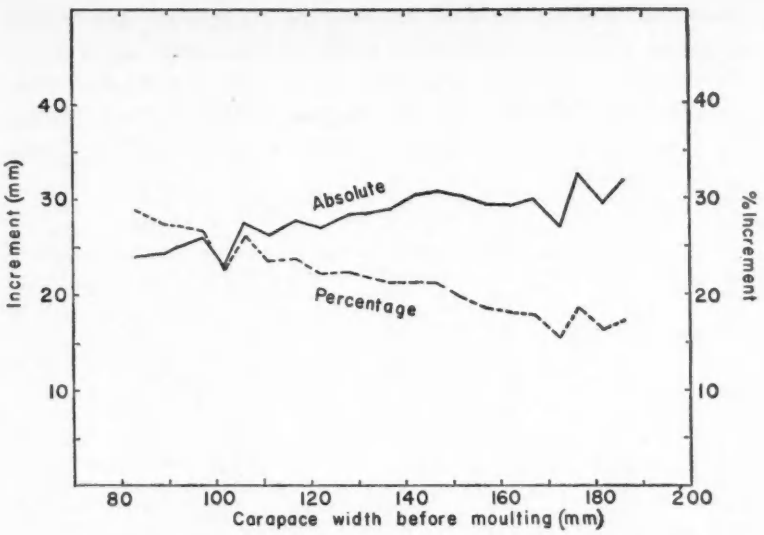

FIG. 3. Absolute and percentage increments at moulting of male crabs.

DETERMINATION OF INSTAR SIZES

For early post-larval stages, and for larger crabs, carapace width before moulting was plotted against carapace width after moulting (Fig. 4). Straight lines were fitted by least squares, of the general form:

$$Y = aX + b \tag{1}$$

Y is carapace width in millimetres after moulting, and X is the same before moulting; a and b are fitted constants.

For unsexed and male (6.63–29 mm):

$$Y = 1.22X + 1.62 \tag{3}$$

For males (83–186 mm):

$$Y = 1.07X + 19.00 \tag{3}$$

For females (88–145 mm):

$$Y = 0.892X + 31.58 \tag{4}$$

Lines (3) and (4) intersect (2). The points of intersection represent inflexions or abrupt changes in growth rate. They may be taken from Fig. 4, or calculated by the method of Kurata (1960), as follows. Let the constants of line (2) above be a and b, and those for (3) or (4) be a' and b'; then the point of intersection of the two lines, L, is:

$$L = \frac{b' - b}{a - a'} \tag{5}$$

The intersects, 115.9 mm for males and 90.8 mm for females, agree reasonably well with sizes at maturity determined earlier (Butler, 1960), hence it is likely that the change in growth rate is associated with sexual maturity. The long extrapolation of line (2) seems justified because it conforms with the general pattern of growth in Crustacea generally (Kurata, op cit.) and for *C. magister* specifically, as shown later.

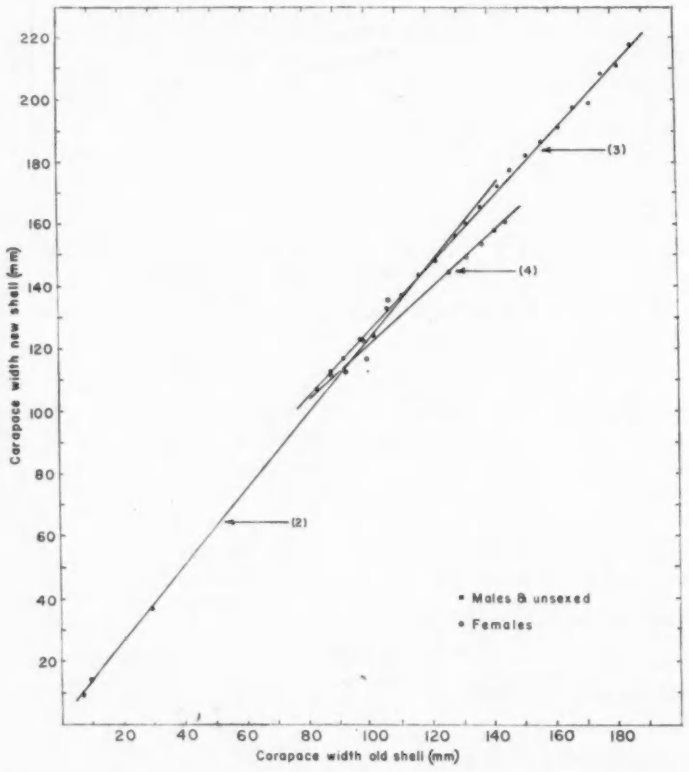

FIG. 4. Increases in carapace width as expressed by equations 2–4 of the text.

Starting with the 2nd post-larval stage at a carapace width of 10 mm, equation (2) was used to calculate instar sizes up to the 12th instar for males; and instars 13 to 16 were determined by equation (3). Likewise, female instar sizes up to the 11th were calculated from equation (2), and the rest up to 16 from (4). Calculated carapace widths are given in Table IV.

TABLE IV. Comparison of instar sizes of *Cancer magister*. Measurements are of carapace widths, including 10th spines.

Instar	Washington (Cleaver)		Southern B.C. (MacKay and Weymouth)		Queen Charlotte Islands	
	♂	♀	♂	♀	♂	♀
No.	*mm*	*mm*	mm	mm	*mm*	mm
1	(5–7)	(5–7)	5.2	5.2	6.9	6.9
2	9.4	9.4	7.4	7.4	10.0	10.0
3	12.5	12.5	9.7	9.7	13.8	13.8
4	16.8	16.8	13.4	13.4	18.5	18.5
5	23.5	23.5	18.2	18.2	24.2	24.2
6	30.4	30.4	24.0	24.0	31.1	31.1
7	37.2	37.2	31.5	31.5	39.6	39.6
8	47.2	47.2	41.0	41.0	49.9	49.9
9	59.8	59.8	52.5	52.5	62.5	62.5
10	72.8	72.8	65.7	65.7	77.9	77.9
11	90.6	90.6	80.5	80.5	96.6	96.6
12	113.4	113.4?	95.8	95.8	119.5	117.8
13	138.4	126.0?	112.6	112.6	146.9	136.6
14	165.9	137.0?	130.0	127.3	176.2	152.5
15	(188?)	...	149.6	141.3	207.5	167.6
16	...	...	170.8	153.5	241.0	181.1
17	...	...	190.1	...	...	...

ESTIMATE OF AGE

The number of instars which both sexes may be expected to pass through has been determined, but no data which bear directly on frequency of moulting or time spent in various instars are available. In an attempt to estimate age, the calculated instar sizes have been superimposed on carapace width frequency distributions. A total of 8,145 crabs were used for this study, collected between 1950 and 1956 by traps, trawls and dip-nets along the beach. Crabs were measured with sliding brass calipers, accurate to the nearest millimeter.

At metamorphosis crabs are about 5 months old, calculated from time of hatching in April. It is not known which stage the early post-larval stages reach before the onset of winter, and whether moulting occurs during the colder months. No sample of juvenile stages has been taken between September and June. Size frequency distributions are shown of both male and female crabs collected near Masset during June, 1950. On June 3 (Fig. 5A, 6A) most individuals appeared to be in the 2nd and 3rd stages; on June 28, 3rd-stage crabs were most prevalent with others apparently belonging to 4th and 5th stages (Fig. 5B, 6B). One other sample taken during June 26–27, 1956 (Fig. 5C) included 4 males between 24 and 43 mm which seemed to be in stages 5 to 7. Four samples collected during the month of July in 1951, 1953 and 1954 (Fig. 5D-F, 6C-E) show males and females from 23 to 70 mm in stages 5 to 9. A sample from Naden Harbour taken from August 29 to September 4, 1954, had males from 43 to 75 mm in stages 7 to 10; and females from 40 to 78 mm which apparently fall into stages

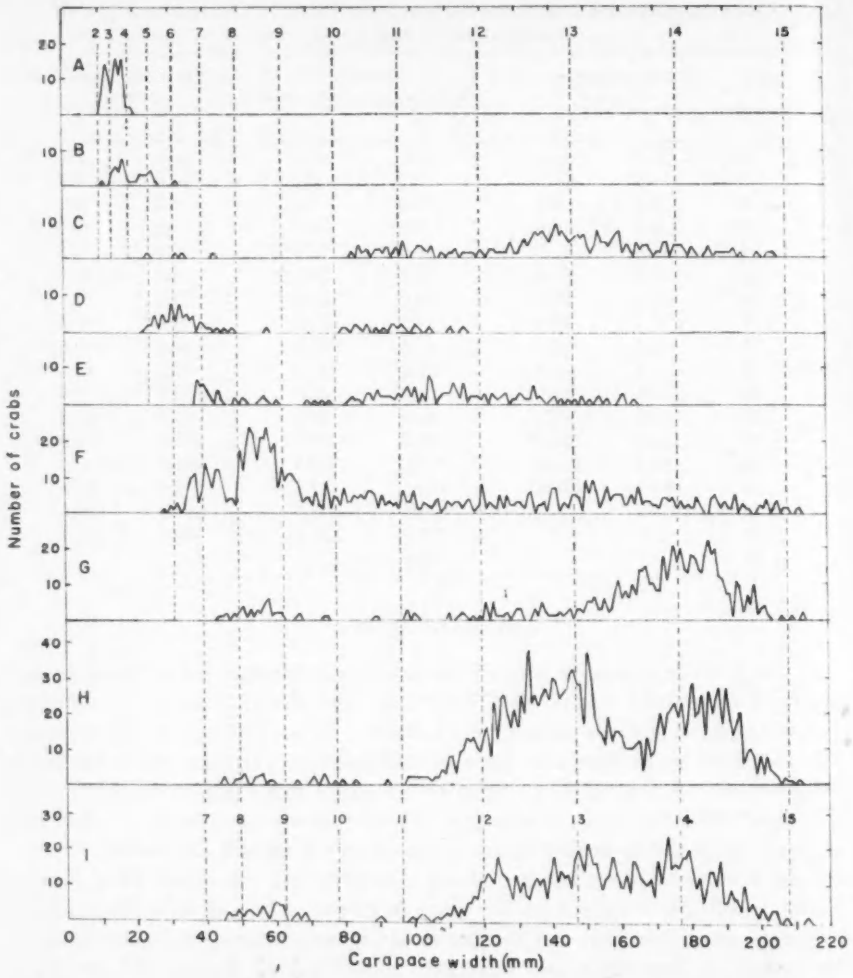

FIG. 5. Carapace width frequency distributions of male crabs collected between June 3, 1950 and September, 1956. Vertical lines represent positions of calculated instars. Sections A and B, Masset, June 3 and 28, 1950; D, Yakan Point, July 12 and 17, 1951; E and F, Hecate Strait, July 9–14, 1954, July 7–20, 1953; C, G, H, I, Naden Harbour, June 26–27, 1956, August 29–September 4, 1954, September 11–23, 1955, September 16–22, 1956.

7 to 10 (Fig. 5G, 6F). In September, 1955, and 1956 (Fig. 5H, I) males from Naden Harbour ranged from 45 to 83 mm which seemed to be in stages 7 to 10 and females (Fig. 6G, H) appeared to fall into stages from 7 to 10.

Thus young crabs which metamorphose in September may range from 15 to 30 mm, stages 3 to 6, by the following June about 8 months later. By the

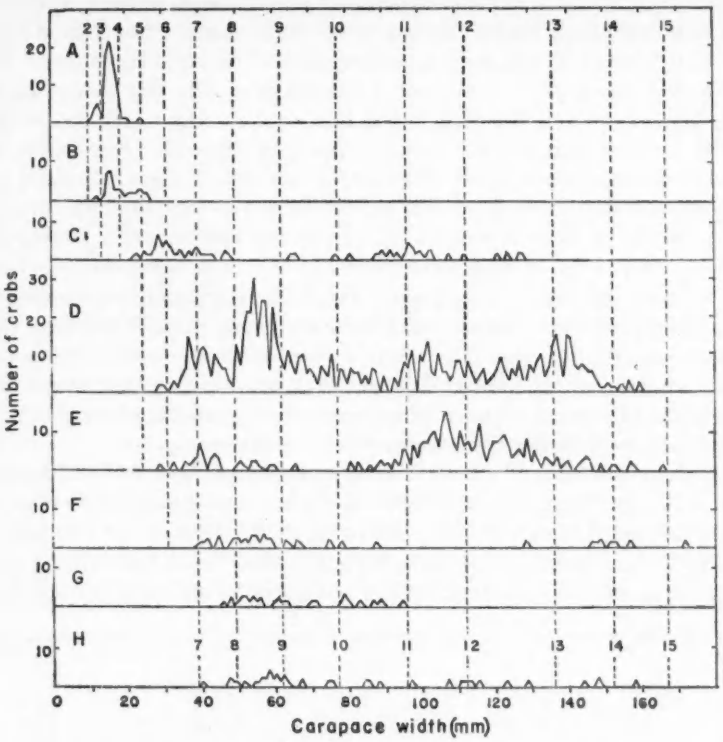

FIG. 6. Carapace width frequency distributions of female crabs collected between June 3, 1950 and September, 1956. Vertical lines represent positions of calculated instars. Sections A and B, Masset, June 3 and 28, 1950; C, Yakan Point, July 12 and 17, 1951; D and E, Hecate Strait, July 7–20, 1953, July 9–14, 1954; F, G, H, Naden Harbour, August 29–September 4, 1954, September 11–23, 1955, September 16–22, 1956.

end of the summer, a year after metamorphosis or about 17 months after hatching the fastest growing individuals in the group may be about 80 mm, and in the 9th or 10th stages.

The combined sample taken on July 12 and 17, 1951, at Yakan Point (McIntyre Bay) and Masset, respectively, shows a group of males between 80 and 115 mm which seemed to fall mostly into stage 11 (Fig. 5D); the majority of females occurred in a group between 80 and 110 mm and probably belonged to stage 11 (Fig. 6C). The frequency distribution of male crabs measured during July, 1954, in Hecate Strait (Fig. 5E) showed a fairly prominent group between 82 and about 115 mm, which seemed mostly to be in stage 11. The picture is less clear for the female distribution in the same sample (Fig. 6E);

individuals of 81 mm and larger were found which may have been in stages 10 to 12. Male crabs from Naden Harbour taken during June, 1956, (Fig. 5C) ranging from 83 to about 130 mm, seem to belong to the 10th and 11th stages. Another sample from the same region about 3 months later (Fig. 5I) shows the lack of males between 80 and 100 mm, in the 10th or 11th stages and the prominence of those between 110 and 130 mm, belonging to stage 12. Also in the sample collected in September, 1955, (Fig. 5H) a paucity of stage 11 males seemed apparent; although there is no clear separation of 110–155 mm males into stages, some grouping of those between 110 and 130 mm is indicated. During August and September, 1954, in Naden Harbour (Fig. 5G) there were relatively few male crabs between 80 and 110 mm, where stage 11 individuals are assumed to be. The same distribution shows a fairly discrete group present between 110 and 130 mm, presumably stage 12. Thus 2 years following metamorphosis, or 29 months after hatching, most male crabs probably have reached stage 12, with fewer in the 11th stage. Fewer measurements are available of females but after 2 years they are probably much the same size as males.

On June 15, 1953, 535 cast-off male exoskeletons from 93 to 175 mm were found at Yakan Point (Fig. 7). There is a prominent group in the distribution between 109 and 138 mm probably belonging mostly to stage 12 with some overlap of 13th stage males. It is likely then that these crabs had reached stage 12 the preceding autumn, passed the winter and spring in this stage and had moulted

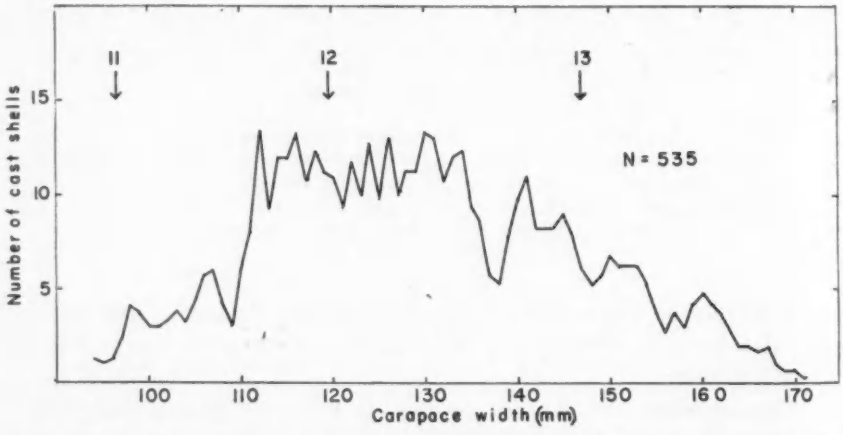

FIG. 7. Cast-off shells of male crabs measured at Yakan Point (McIntyre Bay) June 15, 1953. Positions of calculated instars shown by numbered arrows.

just prior to sampling. A small number of males about to moult and soft-shelled specimens observed at the same time indicate that the sample of cast-off exoskeletons represented current conditions. Figure 8 shows a sample of male crabs caught in McIntyre Bay early in July, 1956, made up entirely of individuals

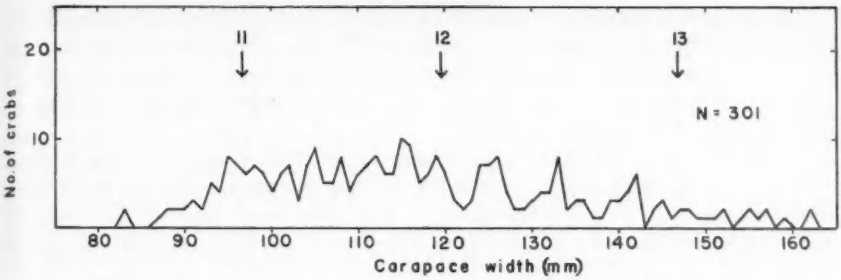

FIG. 8. Carapace width frequency distribution of male crabs, about to moult, McIntyre Bay, July 4–5, 1956. Positions of calculated instars shown by numbered arrows.

about to moult[2]. These males range from 83 to 162 mm but there is an indication of a group between 92 and 122 mm apparently in stages 11 and 12. Thus, both 1953 and 1956 samples are evidence that passage from the 12th to the 13th stage occurs during early summer, and moreover there is no indication that these males, now in their fourth summer, will moult again for another year. Samples from Naden Harbour during September, 1956 and 1955 (Fig. 5G, H), have definite groups, about 130 to 155 mm, which seemed to consist of stage 13 males, attained 3 years after metamorphosis or about 41 months after hatching.

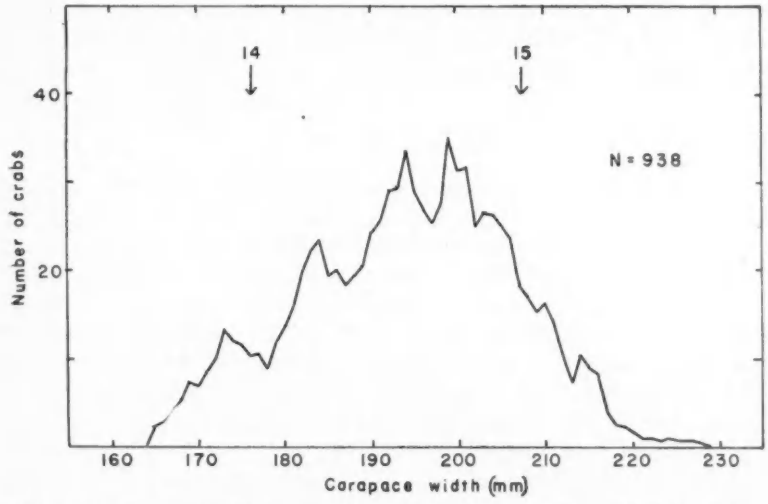

FIG. 9. Carapace width frequency distribution of male crabs sampled from commercial catch, McIntyre Bay, May 16, 1956. Positions of calculated instars shown by numbered arrows.

[2]In these males the carapace had separated along the pleural groove or epimeral line on the antero-lateral and postero-lateral margins; and there was splitting along the absorption lines on the large segments of the chelipeds.

Maturity of females is reached at a carapace width of about 100 mm (Butler, 1960) in the 11th or 12th stages at the end of 2 years; after then, it is not certain whether females moult annually. Measurements of larger females are mostly lacking but that ecdysis is less frequent is indicated by observations of fouling on exoskeletons, which at times is heavy.

If it be postulated that males remain in the 13th stage for about a year, then stage 14 is reached during the 5th summer between 4 and 4½ years after hatching. Groups of males belonging to this stage seem apparent in the 1955 and 1956 Naden Harbour samples (Fig. 5H, I) and the May 16, 1956, sample of

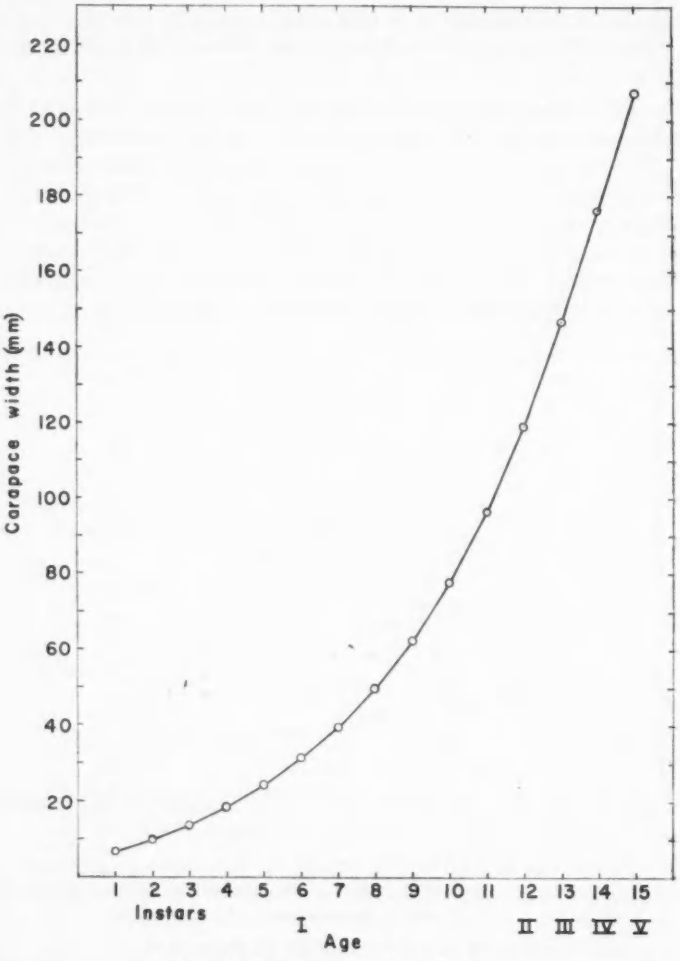

FIG. 10. Growth curve of male crabs.

the commercial catch from McIntyre Bay (Fig. 9). In this latter sample there is undoubtedly overlap between stages, but it seems likely that males of 200 mm and larger belong to stage 15. Probably most males spend about a year in stage 14, but tag recoveries indicate that some individuals may not moult for 2 years. The majority of males then seem to reach the 15th stage after 5 years, the rest after 6 or even 7 years. The estimated size of stage 16 is 241 mm but the largest male on record from the Queen Charlotte Islands measured 235 mm. Therefore, it is likely that stage 16 is rarely, if ever, attained and that stage 15 is in effect the final one in the crab's life. How long the crab lives after reaching the 15th stage is uncertain. Several large tagged males have been recovered after periods of freedom from 12 to 20 months, but the general lack of fouling on large male crabs seems to indicate that usually duration of the stage is no more than a year. Probably then males generally reach stage 15 after 5 years and live for a year longer; and even if moulting is less frequent in the latter stages, the maximum age is no more than 8 years.

In Figure 10 carapace widths of male crabs are plotted against stage number. An age scale in years is placed along the abscicca making the graph in effect a growth curve.

COMPARISON WITH EARLIER GROWTH STUDIES

In Table V present calculated stage sizes are compared with those determined earlier by MacKay and Weymouth (1935) and Cleaver (1949). All measurements of carapace width include the 10th antero-lateral spines. Cleaver's lengths for males and immature females were converted using an equation calculated from data of Weymouth and MacKay (1936):

$$Y = 0.0715X - 0.029$$

Y = combined length in cm of 10th antero-lateral spines; X = carapace width in cm exclusive of spines. Stage sizes of mature females were converted by taking spine lengths from the Fig. 9 in the same paper cited above.

The size of the first post-larval stage, 5.2 mm as given by MacKay and Weymouth, is lower than values of Cleaver and the present paper, between 5 and 7 mm and 6.9 mm, respectively. Also Waldron (1958) reported that 1st-stage crabs, moulting from the megalops, ranged from 6.6 to 8.3 mm. Thus it seems that the first 2 stages reported by MacKay and Weymouth should be combined so that the size range of stage 1 is between 5 and 8 mm. If their stage 3 at 9.7 mm is considered as stage 2, then it becomes comparable with Cleaver's 2nd stage at 9.4 mm and the 2nd stage here at 10 mm. Also, if successive stages are set back accordingly, then differences between stage sizes as found by Cleaver and by Mackay and Weymouth are not great, at least until after stage 12. That is, between stages 2 and 11 the stage sizes and increments determined by the latter workers are larger; stage 12 sizes differ by less than a millimeter; but in following stages the sizes and increments reported by Cleaver are somewhat greater. Thus

TABLE V. Comparison of average growth in width of carapace in male crabs from Queen Charlotte Islands with those obtained in Washington by Cleaver (1949). Measurements include 10th spines.

Washington			Queen Charlotte Islands		
Size	Crabs	Growth	Size	Crabs	Growth
mm	*No.*	mm	mm	*No.*	mm
21.0–30.6	25	6.4	29	1	8
74.5–84.2	6	19.9	80–84	1	24
85.3–94.0	19	21.5	85–89	3	24.4
			90–94	2	25.0
96.2–105.8	23	22.7	95–99	6	26.0
			100–104	2	22.0
107.0–116.7	51	22.7	105–109	3	27.6
			110–114	3	26.3
118.0–127.4	19	23.2	115–119	3	27.7
			120–124	2	27.0
128.6–138.4	8	24.7	125–129	7	28.4
			130–134	15	28.6
			134–139	11	29.2
139.6–149.1	6	25.3	140–144	22	30.4
			145–149	32	31.9
150.1–160.1	2	21.5	150–154	43	30.3
			155–159	53	29.4
161.2–171.0	1	24.0	160–164	43	29.4
			165–169	15	30.0

stage sizes as determined by these authors are similar if the assumption may be made concerning the grouping of the first two stages of MacKay and Weymouth. However, growth per moult and calculated stage sizes reported here for the Queen Charlotte Islands are larger than above values.

That actual increments reported here are larger seems attributable to the fact that moulting mostly occurred under natural conditions. Twenty-two males and 5 unsexed early post-larval crabs moulted in captivity. Twelve recovered tagged males moulted under natural conditions, and apparently the tag did not retard growth. The other male and all female records were obtained from crab traps. It might be argued that a trap constitutes an artificial surrounding, but it is obvious that crabs may enter freely and moult without the disturbances of being moved to a live-well or aquarium where water temperatures and salinity might differ.

MacKay and Weymouth tried to approximate natural conditions, but they state " . . . . the increase of crabs in live-boxes was only about three-fourths of the normal among the smaller individuals". Practically no natural moulting records of larger crabs were obtained. Cleaver stated that only crabs which

moulted within a day after recapture were considered but Table V shows that, over approximately the same range, increments found here were larger than Cleaver's except in one group between 100 and 104 mm. Waldron (1958) obtained 102 moulting records (individuals less than about 32 mm, unsexed) in captivity at Newport, Oregon. He reports a similarity between these and Cleaver's data which is supported by his figure 13; but increments obtained at Newport are generally lower. Thus it seems reasonable to conclude that increments found in the course of earlier work were lower because moulting occurred mostly under artificial conditions. Kurata (1960) calculated growth equations for *C. magister* using data from MacKay and Weymouth, and I have calculated equations from Cleaver's moulting records. Constants of these equations are given in Table VI.

TABLE VI. Constants, *a* and *b*, of growth equations calculated from other authors.

	Juvenile		Male		Female	
	a	*b*	*a*	*b*	*a*	*b*
MacKay and Weymouth	1.1980	0.7068	1.1121	5.639	0.9343	22.735
Cleaver	1.23	0.57	1.02	20.6	0.849	34.03

For juveniles, constants shown above differ slightly, mostly in b values, from those calculated in equation (2); but the straight lines represented here are essentially similar. Cleaver's moulting juveniles included 130 unsexed individuals and males from 5.10 to 90.8 mm (converted values of class mid-points). The intercepts, or points of change in growth rate, determined from Cleaver's data, were 100.2 mm for males and 90.2 mm for females. These points approximate those calculate in this paper, but they differ appreciably from intersects (57.4 mm[3] for males and 83.5 mm for females) derived from the data of MacKay and Weymouth. Kurata observes that the latter intercepts do not approach the size for attainment of maturity, about 100 mm, reported by these authors. Inspection of Kurata's figure 25C suggests that the intercept for males might be better placed at about 85 mm, and he does state that an inflexion at about 60 mm is not distinct. In any case, each growth study of *C. magister* has shown that growth rate does change at or near sexual maturity. And since line (2) and its intercepts with (3) and (4) are in fairly good agreement with those obtained from Cleaver's records, there is support for using its equation as a means of calculating growth by instars.

Ages determined here are much the same as those found by Cleaver. He concluded that age in years, from hatching, may be assigned to size as follows: after 1 year, 37.2 mm; after 2 years, 113.4 mm; after 3 years, 165.9 mm; and after 4 years, most males reached commercial size. However, according to Cleaver, 15 stages are required for attainment of commercial size as compared with the 14 stages estimated here.

[3]Reported by Kurata as 64.46 mm.

MacKay and Weymouth in their figures 5 and 6 show the following carapace widths (mm) of males at various ages:

Age	*Carapace*	*Age*	*Carapace*
1	10	5	115
2	60	6	130
3	85	7	150
4	100	8	165 (legal size, B.C.)

Their starting point for age determination is not stated clearly, but seems to be when fertilized eggs are extruded. In any case the discrepancy here is less than 6 months and cannot account for a growth rate only about half that of Cleaver's or our Fig. 10. However, there is evidence in MacKay and Weymouth's paper of a more rapid growth, at least for the first 2 years. They state that a sample collected in September (shown in their figure 3) contains 3 age groups: early post-larval stages or young of the year at 10 or 20 mm; yearlings at 40 to 70 mm; and 2-year-old crabs at 100 to 120 mm. These estimates contradict their main argument and conclusions concerning age determination, but agree reasonably well with Cleaver's and the present age estimates.

SUMMARY

1. Data are presented on growth of the Pacific edible crab and an attempt is made to estimate age of crabs in the Queen Charlotte Islands region.

2. A total of 2,820 early post-larval crabs were collected by small-meshed trawl from 1953 to 1956 in McIntyre Bay and Naden Harbour.

3. Five post-larval unsexed crabs moulted; increments of carapace width were from 36.3 to 46.5%. In a sample of 1,175 unsexed crabs, modes at 6.9 and 10 mm were identified as 1st and 2nd instars, respectively.

4. Moulting records of larger crabs were obtained as follows: from 1953 to 1957, 250 males and 44 females moulted in crab traps; in 1956 and 1957, 22 males moulted in live-wells; and between 1955 and 1959, 12 tagged males moulted while at large. Size range of moulting males was from 83 to 186 mm; females from 88 to 145 mm.

5. For each sex, carapace widths of early post-larval and larger crabs before moulting were plotted on arithmetic scale against carapace widths after moulting, to produce straight lines. Using equations of these lines and size of the 2nd stage, average carapace widths were calculated for stages 3 to 16.

6. In width frequency distributions of 8,145 crabs separation of stages was sufficient for identification of age groups. From seasonal occurrence of groups and indication of moulting frequency from tag recoveries, it is estimated for male crabs that a year after hatching stage 5 or 6 is reached; after 2 years stage 11 or 12 is attained; after 3 years most crabs are in the 13th stage; after

4 years stage 14 is reached; and generally at the end of 5 years crabs are in stage 15. Growth of females appears similar for the first 2 years but afterwards is slower.

7. Both sexes reach sexual maturity in the 11th or 12th stages after 2 years. Males reach commercial size in stage 14 after 4 years. Probably the maximum age of crabs is 8 years.

ACKNOWLEDGMENTS

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APPENDIX TABLE A. Carapace widths of post-larval crabs, McIntyre Bay, August 29 to September 9, 1953.

mm	*No.*	*mm*	*No.*	*mm*	*No.*	*mm*	*No.*	*mm*	*No.*
5.8	1	8.1	2	10.4	35	12.7	1	15.0	1
.9	2	.2	0	.5	25	.8	1	.1	0
6.0	5	.3	1	.6	36	.9	1	.2	1
.1	6	.4	0	.7	26	13.0	1	.3	1
.2	16	.5	0	.8	26	.1	0	.4	0
.3	13	.6	2	.9	18	.2	2	.5	0
.4	29	.7	2	11.0	11	.3	7	.6	0
.5	40	.8	1	.1	10	.4	3	.7	3
.6	43	.9	3	.2	5	.5	3	.8	0
.7	36	9.0	11	.3	10	.6	1	.9	1
.8	67	.1	7	.4	3	.7	2	16.0	0
.9	74	.2	7	.5	7	.8	0	.1	1
7.0	63	.3	8	.6	7	.9	1	.6	1
.1	50	.4	11	.7	1	14.0	2	18.3	1
.2	34	.5	14	.8	2	.1	7	.5	1
.3	28	.6	19	.9	1	.2	2	19.5	1
.4	24	.7	27	12.0	1	.3	1	.8	1
.5	5	.8	27	.1	1	.4	3	20.1	1
.6	5	.9	35	.2	0	.5	2	.7	1
.7	2	10.0	32	.3	1	.6	3	21.0	1
.8	2	.1	41	.4	1	.7	1	.4	1
.9	1	.2	30	.5	1	.8	1		
8.0	0	.3	32	.6	0	.9	1		

APPENDIX TABLE B. Moulting records of tagged male crabs, released during 1955, 1956 and 1957 and recovered in 1956, 1957, and 1959.

Carapace width		Increment	
Old	New		
mm	*mm*	*mm*	*%*
144	178	34	23.6
146	178	32	21.9
155	180	25	16.1
158	174	16	10.1
159	190	31	19.5
160	174	14	8.8
163	193	30	18.4
164	193	29	17.7
165	193	28	17.0
168	200	32	19.1
172	202	30	17.4
172	203	31	18.0

APPENDIX TABLE C. Records of male crabs moulting in live-wells at Masset, 1956 and 1957

Carapace width		Increment	
Old	New		
mm	*mm*	*mm*	%
	1956		
83	107	24	28.9
92	115	23	25.0
98	124	26	26.5
105	135	30	28.6
115	140	25	21.7
133	164	31	23.3
136	163	27	19.9
147	174	27	18.4
160	186	26	16.3
160	188	28	17.5
167	199	32	19.2
174	201	27	15.5
	1957		
97	121	24	24.7
103	124	21	20.4
110	138	28	25.5
129	153	24	18.6
131	154	23	17.6
131	160	29	22.1
132	159	27	20.5
136	164	28	20.6
150	179	29	19.3
160	188	28	17.5

1 Corinthians 13:13